How flower visitation of remnant grassland patches is affected by commercial timber plantations and an invasive alien species (*Rubus cuneifolius*)

by

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Declaration

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General summary

Our planet is in the midst of a biodiversity crisis, with factors such as land transformation, climate change, anthropomorphic disturbance and invasive species acting together to threaten biodiversity. In South Africa, with minimal natural wood resources, commercial forestry is one of the most abundant forms of landscape transformation. However, a third of the land inside many plantations has been set aside for conservation as unplanted remnant grassland patches (RGPs). These areas are subjected to an additional negative impact by invasive alien species, namely *Rubus cuneifolius* (American bramble), a weed that is particularly problematic in and around forestry plantations in South Africa. The grassland biome of South Africa is extremely diverse and is of vital importance for the ecosystem services it supplies. Despite this, the grassland biome is under threat as this is where much of South Africa's forestry plantations are located. Driven by anthropomorphic disturbance, pollinators are in decline. Landscape transformation of natural areas for forestry plantations is likely to affect plant-pollinator interactions which will affect ecosystems and biodiversity. However, it is not known to what extent these ecosystems are affected. It is thought that the impact depends on the complexity of the ecosystem in question, and analyses at the network-level provide insights into the robustness of ecosystems in the face of biodiversity loss. Thus, this study evaluates the effect of natural habitat fragmentation and invasion of the alien species, *R. cuneifolius*, on flower visitation networks of South African grasslands.

The study was conducted in the KwaZulu-Natal Midlands within a commercial timber plantation and a neighbouring protected area (PA). Flower-visitor observations were carried out in uninvaded protected areas and RGPs and in protected areas and RGPs invaded by *R. cuneifolius*. I found that RGPs within commercial forestry plantations successfully decrease the negative effects of land transformation on the grasslands of the KwaZulu-Natal Midlands, and flower visitation network patterns are largely maintained in these habitat fragments. However, within RGPs, invasion by *R. cuneifolius* affected the composition and the interaction network structure of flower-visitor and plant communities.

The fact that there are unplanted areas within commercial forestry plantations is positive for biodiversity conservation in South Africa. Research has indicated that these areas successfully aid in the conservation of biodiversity and ecosystem functioning. Due to the positive influence that RGPs have on conservation in fragmented and transformed landscapes, it is critical that these unplanted areas are retained. However, the effects of bramble invasion are more intense within RGPs than within protected areas, and therefore, it must be a priority to keep these areas undisturbed. *R. cuneifolius* has been found to have devastating effects on ecosystem function and network structure. It is also a category 1 invasive plant within South Africa, and its removal is required by law. Therefore, the removal of bramble must be a management priority.

Algehele samevatting

Ons planeet is in die middel van 'n biodiversiteit krisis, met faktore soos grond transformasie, klimaatsverandering, antropomorfiese versteuring en indringerspesies wat gesamentlik werk om biodiversiteit te bedreig. Suid-Afrika, besit minimale houtbronne. Daarom is kommersiële bosbou een van die mees algemene vorme van landskap transformasie. Tog is 'n derde van die land binne baie plantasies opsy gesit vir bewaring as oorblywende grasveld kolle (OGKs). Hierdie gebiede word ongelukkig blootgestel aan die bykomende negatiewe impak van die uitheemse spesies, *Rubus cuneifolius* (Amerikaanse steekdoring), wat veral problematies is in en rondom bosbouplantasies. Die grasveldbioom van Suid-Afrika is baie divers en is van kardinale belang vir die ekosisteem dienste wat dit lewer. Ten spyte hiervan, word die grasveldbioom bedreig waar dit op dieselfde areas as die meerderheid van Suid-Afrika se bosbouplantasies geleë is. Antropomorfiese versteuring lui daartoe dat bestuiwergetalle daal. Landskap transformasie vir bosbou plantasies raak dus plant-bestuiwer interaksies, wat ekosisteme en biodiversiteit beïnvloed. Dit is nie bekend tot watter mate hierdie ekosisteme geraak word nie. Daar word vermoed dat die impak af hang van die kompleksiteit van die ekosisteem. Ontledings van ekosisteme op netwerk vlak kan insigte bied oor die robuustheid van hierdie ekosisteme in die aangesig van biodiversiteitverlies. Dus, die studie evalueer die effek van fragmentasie van natuurlike habitatte en inval van die indringer spesie, *R. cuneifolius*, op blom-besoekings netwerke van Suid-Afrikaanse grasvelde.

Hierdie studie is uitgevoer in die KwaZulu-Natal Midlands binne 'n kommersiële hout plantasie en 'n naburige beskermde gebied (BG). Blom-besoeker waarnemings was in BGs en OGKs sonder *R. cuneifolius*, en in BGs en OGKs met *R. cuneifolius* uitgevoer. Ek het gevind dat OGKs binne kommersiële bosbouplantasies suksesvol is om die negatiewe uitwerking van land transformasie te verminder, en blom-besoeking netwerk patrone grootliks gehandhaaf word in hierdie habitat fragmente. Egter, binne OGKs, het *R. cuneifolius* die samestelling en die interaksie netwerk struktuur van blom-besoekers en plant gemeenskappe negatief geraak.

Die feit dat OGKs ongeplant gelaat word, is positief vir die bewaring van biodiversiteit in Suid-Afrika. Navorsing dui aan dat hierdie gebiede suksesvol is om te help met die bewaring van biodiversiteit en ekosisteemfunksionering. As gevolg van die positiewe invloed van OGKs op bewaring in gefragmenteerde en omskepte landskappe, is dit krities dat hierdie areas ongeplant bly. Egter, die gevolge van steekdoring inval is meer intens binne OGKs as binne beskermde gebiede, en daarom moet dit 'n prioriteit wees om hierdie gebiede ongestoord te hou. *R. cuneifolius* se verwoestende uitwerking op ekosisteem funksie en netwerk struktuur was baie duidelik. Dit is ook 'n kategorie 1 indringerplant in Suid-Afrika, en sy verwydering word deur is die wet vereis. Daarom moet die verwydering van steekdoring ‘n bestuursprioriteit wees.

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Dedication

This thesis is dedicated to George Nieuwoudt, and to my whole family. Thank you for getting me through the hard times.

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CHAPTER 1
General Introduction

The biodiversity crisis

Biodiversity is the base upon which human survival depends. It is a great asset to humankind, providing us with enormous benefits including economic gain, a wide range of essential indirect services, and maintenance of ecosystem stability and functioning (Singh, 2002). Biodiversity is also responsible for essential ecosystem services including regulation of atmospheric gas, climate, water, disturbance, pollution, soil formation and fertility, pollination, waste assimilation and recreation (Costanza, 1997). Mass extinction events are characterized by the loss of more than 75% of the Earth's biodiversity over a geologically short time-period (Barnosky et al., 2011). There have been five previous extinction events, all of them naturally occurring, however, modern extinctions of species and populations suggest we are currently in a sixth mass extinction event, this time induced by humans (Barnosky et al., 2011). Much of the Earth's surface has been transformed by human activities involving extensive destruction of natural habitat, and even where habitats remain, they are often degraded with assemblage structures that have been exploited and altered (Gaston et al., 2008). Habitat loss, fragmentation, overexploitation of natural resources, pollution, climate change and the spread of invasive alien species are recognised as the greatest threats to global biodiversity (Barnosky et al., 2011). Habitat fragmentation, a multidimensional issue that can simultaneously involve the loss of habitat, a shift toward smaller patches and an increase in the distances separating patches, is described as the most serious threat to the maintenance of biological diversity (Wilcox & Murphy, 1985; Wiens, 1989).

Connecting the landscape

Intact and connected ecosystems are important so that ecological integrity and processes can be maintained over the long term for conservation value and the provision of critical ecosystem services for humans and other species (Bennett, 1999). Properly connected habitats facilitate the movement of organisms, genetic interchange and other ecological flows that are vital for the survival of species and for the conservation of biodiversity in general (Crooks & Sanjayan, 2006). Fragmented habitats create discontinuities in ecological processes that alter the flow of ecosystem services, to the detriment of ecosystem health and human well-being (Aronson et al., 2007). Thus, ensuring continuity and heterogeneity of natural areas is one of the most

important aspects for conserving biodiversity at the landscape level, and should be a goal in all conservation areas. While protected areas remain the cornerstone of biodiversity conservation, the importance of maintaining biological diversity within transformed landscapes is becoming increasingly clear (Gaston et al., 2008). Protected areas in isolation face serious issues over the long term. Isolated areas of natural habitats can, in many regions, be looked upon as "islands". The smaller and the more isolated they are, the more likely species are to decline (Jongman et al., 2004). This isolation leads to metapopulation breakdown, where populations become isolated, leading to genetic inbreeding depression, stochastic extinction, localised resource overuse and susceptibility to introduced diseases, ultimately leading to localised extinctions (Diamond, 1984; Hanski, 1998). This, combined with no recolonisation events, can result in regional extinction (Hanski, 1998).

The survival of species is dependent on habitat quality, availability of food and, for many species, the ability to move through the landscape (Hansson et al., 1992). Movement of organisms is necessary for many reasons, including: i) to enable successional processes; ii) to provide enough space for species with large home ranges; iii) to ensure large enough population sizes when individual sites are small; iv) to ensure that recolonisations can take place where presently unoccupied sites may be vital to a species in the long-term; v) to ensure protection for all the stages of a species life cycle; vi) to facilitate migratory behaviours; and vii) to enable the distributions of species to shift in the event of environmental change (Gaston et al., 2008).

Global use of remnant patches

Ecological networks are defined by Jongman (1995) as strips of remnant habitat designed to connect protected areas and other areas of high natural value across transformed landscapes. These are configured as matrixes of remnant patches which consist of interconnected patches of natural habitat (such as remnant forest or grasslands), special landscape features (including hilltops and wetlands) and managed areas such as firebreaks and underneath electricity lines (Samways et al., 2010). Together, the different landscape features of remnant patches offset the negative effect that transformed landscapes have on native biodiversity as they enable persistence and movement of individuals and propagules through the transformed matrix at the landscape spatial scale (Kirkman & Pott, 2002; Samways**,** 2007; Joubert et al., 2014). Remnant habitat patches can function as conduits, habitats, filters, barriers, sources or sinks for biodiversity (Hess & Fischer, 2001). Conduits were defined by Hess and Fischer (2001) as areas that enable organisms to move through the corridor from one place to another, and

habitats are an area with the appropriate combination of resources and environmental conditions to support life. Filters and barriers separate areas on opposite sides of a corridor (Forman, 1995). Sources are defined as habitats in which local reproduction exceeds mortality, and sinks as habitats in which mortality exceeds reproduction (Shmida & Ellner, 1984; Pulliam, 1988).

Matrixes of remnant patches provide a possible solution for maintenance of biological diversity within altered landscapes, where conservation is often of lower priority, mitigating the isolation of populations of species affected by habitat fragmentation by facilitating genetic exchange, thus increasing the chances of survival of threatened species. This idea of natural patches has been extensively implemented in Europe, where they are also referred to as greenways (Jongman et al., 2004). Within Europe, creating networks of remnant patches is one of the leading objectives in the Pan-European Biological and Landscape Diversity Strategy (Council of Europe, 1995). In the 1980s, some of the first countries to investigate and promote this strategy were Hungary, the Netherlands and the Czech Republic, and since then matrixes of remnant habitat have gained increasing attention in many additional European countries (Rientjes & Roumelioti, 2003). In Germany, the Bavarian-Sand-Axis EN, an area spanning 2000 km^2 and five cities, protects and connects habitats characterised by dry and sandy soil and sparse vegetation cover (Weinbrecht & Konopka, 2002). This diverse network includes natural habitats such as sand dunes and sand bars along streams, and man-made habitats including extensively grazed grasslands, margins of dry pine forests, field margins, sand pits, and sand-dominated highway verges and railroad tracks (von Haaren & Reich, 2006). The Kronsberg area is part of the greenbelt surrounding Hannover in Germany where intensive agriculture was the dominant land use until the end of the 1980s (Brenken et al., 2003). Today, the Kronsberg must fulfil several purposes: recreational and climatic functions for the residential area, habitat functions for general nature conservation (particularly for several rare or endangered species) as well as farming, with the aim of the project to counteract further loss of open spaces by developing a concept for integrated or “multifunctional” land use (Brenken et al., 2003).

South African remnant patches

There is potential for matrixes of remnant patches to fulfil similar functions as those in Europe within the commercial forestry plantations of South Africa. During the late 1800s, the first alien forest plantations were established in South Africa in response to the country’s

insufficient natural wood sources (Tewari, 2001). Currently, the forestry industry occupies 1.8 million ha in South Africa (DWAF, 2006). The majority of suitable land for forestry is within the grassland, wetland and forest biomes, all of which are severely threatened (Eeley et al., 2002; Neke & du Plessis, 2004; DWAF, 2006). During the 1990s, European forestry companies anticipated that demand for products manufactured in environmentally and socio-economically friendly ways would grow, and thus began the process of certification (Samways et al., 2010). By the mid-1990s, the two largest paper companies in South Africa, Mondi and Sappi, had implemented Forest Stewardship Council (FSC) international standards (Kirkman & Pott, 2002). This required them to conduct forestry in a sustainable way to minimise the effects of commercial forestry on biodiversity. Approximately 500,000 ha of South Africa's commercial forestry plantation land has been left unplanted, most of which occurs in the grassland biome; these areas are maintained mostly as conservation areas (Samways, 2007; Samways et al., 2010). Globally, commercial forestry is a rapidly expanding and often overlooked threat to biodiversity (Brokerhoff et al., 2008). Plantation forestry using alien species poses a serious risk to local biodiversity as exotic trees contain little indigenous biodiversity, and in response, matrixes of remnant habitat patches aim to minimise the negative effects of these plantation forestry blocks through improving connectivity between natural habitats (Samways & Moore, 1991; Beier & Noss, 1998; Pryke & Samways, 2009; Bremer & Farley, 2010; Samways, et al., 2010). The maintenance of remaining native fragments have also been suggested for use within agricultural areas to facilitate pollination of crops such as mango and sunflowers (Carvalheiro et al., 2010; 2011; 2012). However, there is little scientific research currently available on the effectiveness of these remnant grassland patches (RGPs) for biodiversity conservation and maintenance of natural ecosystem function (Samways et al., 2010). While it is known that there are adverse effects of alien plantation trees on compositional biodiversity at the local scale, there is a need to determine the effectiveness of these RGPs at conserving biodiversity at the landscape scale, and in maintaining a close-to-natural state within the unplanted portions of forestry plantations (Samways et al., 2010).

Alien invasive species

The introduction and spread of non-native species has become a global ecological and conservation crisis (Gurevitch & Padilla, 2004). Invasions by alien plants are a growing challenge worldwide to the management of native biodiversity and ecosystem functioning (Brooks et al., 2004). Invasive alien plants (IAPs) are often exceptional competitors that can impact native species in many ways, competing for nutrients, water, light, and space, causing

changes in both faunal and floral composition and structure (Delph, 1986; Newsome & Noble, 1986; Vitousek, 1990; Walker & Vitousek, 1991; Wardle et al., 1994; Weihe & Neely, 1997; Richardson et al., 2000). Many invasive grasses modify natural fire regimes and species composition (D'Antonio & Vitousek, 1992; Hobbs & Huenneke, 1992). For example, Salt-cedar alters fluvial geomorphology, nutrient cycling, fire regimes, and native species regeneration rates (D'Antonio & Vitousek, 1992). This type of vegetative competition may reduce the ability of native species to maintain and increase their population size (Huenneke & Thomson, 1995). IAPs can affect endemic species on many scales, both directly and indirectly. On the ecosystem level, IAPs can cause changes in geomorphological processes such as erosion rate and sedimentation rate (Macdonald et al., 1989; Vitousek, 1990). IAPs may also affect hydrological processes such as water-holding capacity, water-table depth and surface-flow patterns and affect biogeochemical cycling processes such as nutrient mineralization and soil chemistry (Macdonald et al., 1989). The presence of IAPs can also affect ecosystems on a community or population level (Macdonald et al., 1989).

Research into alien plant invasions has increasingly focused on the disturbance effects that IAPs have on pollination networks within ecosystems (Memmott & Waser, 2002; Lopezaraiza-Mikel et al., 2007). Competition for pollination by IAP species may reduce the reproductive capacity of native plants (Brown et al., 2002). IAPs can affect both quantity and quality of pollination services to naturally-occurring plant species (Waser, 1978; Rathcke, 1983). Invasive species with favourable flowering characteristics may draw pollinators away from native species, decreasing visit quantity (competition), or they might increase visitation rate to natives by attracting pollinators which otherwise would not visit the native species as often (facilitation) (Waser, 1978; Thomson, 1978; Brown & Kodric-Brown, 1979; Rathcke, 1988). The quality of pollination service can be affected when flower-visitors pollinate multiple species and deploy mixed loads of pollen, and when flower-visitors move between species and lose or waste pollen (Brown et al., 2002).

Although invasive alien plants are widespread throughout South Africa, their impact, although significant, is not yet fully understood. Previous studies of pairwise interactions have shown that alien plants can affect pollination and flower visitation of native plant species, especially if there are shared pollinators (Lopezaraiza-Mikel et al., 2007). It has been found that the ability of a plant species to affect co-flowering species was increased in species with an abundance of resources, such as more floral units and nectar sugar content, and more accessible flowers

(Carvalheiro et al., 2014). Gibson et al. (2012) found that the effect of an invasive alien plant on the community was determined by the similarity of their floral traits; the more similar the flower of the alien to the native species, the more the visitation to the native species is reduced. Similarly, Carvalheiro et al. (2014) found that the potential influence of an alien plant species to affect plant species with shared pollinators was increased when the alien was phylogenetically closer to the native species. Research suggests that IAPs often infiltrate pollination networks by forming links with generalist species, or by behaving as generalists themselves, directly affecting insect populations and pollination success of naturally-occurring plant species, through competition or facilitation.

The invasive alien plant *Rubus cuneifolius* in South Africa

Rubus cuneifolius, also known as American bramble, is endemic to North America (Pamfil et al., 2010), and has been identified as a troublesome invasive species in South Africa. It is a Declared Weed and category 1 invasive (Conservation of Agricultural Resources Act, 1983) in South Africa, and is one of the top ten most prominent invaders of grasslands (Henderson, 2007). It is a deciduous perennial shrub producing biennial, curved, prickly shoots with leaves occurring in groups of 3 or 5 and white flowers which develop fruit (blackberries) in the second year of growth (Campbell et al., 1992; Denny, 2005). It is also plentiful in the commercial forests in the KwaZulu-Natal Midlands, the focal area for this thesis (Erasmus, 1984; Morris et al., 1999). Brambles have extensive networks of fine roots just below the surface of the soil and it spreads predominantly via vegetative means (Denny, 2005). Bramble responds to disturbance with a period of rapid and prolific growth, making it expensive, time consuming and difficult to control (Boring et al., 1988). A three-phase control method for *R. cuneifolius* has been compiled and tested by Denny (2005): (i) pre-treatment - burning, slashing or flattening the bramble to make treatment possible, (ii) treatment of dense growth- stems are cut off 2-3 times a year in order to prevent nutrients being stored in the roots, thereby starving the roots, and herbicide is used, kill root buds, and (iii) treatment of regrowth and scattered stems- preferably the spraying of a herbicide, or repetition of the second step, until there is no regrowth (Erasmus, 1984; Byford-Jones, 1990; Denny, 2005).

The establishment of bramble thickets within production landscapes is very undesirable. The plant forms impenetrable barriers with its thorny canes, thereby restricting access to the forestry plantations for operations such as thinning, planting, felling and firefighting (Erasmus, 1984). A study conducted by Reynolds & Symes (2013) examining the clearing of invasive bramble

on grassland birds and vegetation in Mistbelt grasslands of KwaZulu Natal, found that; bramble-invaded sites had lower richness and diversity than uninvaded or cleared sites; the presence of bramble had detrimental effects on specialist grassland species; and that clearing initiatives prove effective in restoring native grassland vegetation structure and grassland bird communities by increasing available habitat. The invasive *R. cuneifolius* is therefore problematic in production landscapes and detrimental to native biodiversity.

Pollination interaction networks

The term "ecological networks" has two meanings in ecology. The first is in the landscape context and, as already discussed above, is the spatial array of corridors and patches which collectively are termed an ecological network (Jongman, 1995). The second meaning is used to refer to maps of interactions between species in food web ecology (Margalef, 1991). These interaction networks are usually in the form of 1) traditional food webs, 2) host-parasitoid webs, and 3) mutualistic webs (Ings et al., 2009), and contain information about which species link with which other species and the strength of these links or interactions (Montoya et al., 2006). A fundamental reason for constructing these networks is to create better understanding about how the complexity of nature can persist and how it affects the functioning of the ecosystem (Ings et al., 2009). Since this study deals with both landscape and interaction ecological networks, different terms have been assigned to both uses of "ecological networks" from this point onwards. The landscape ecology term, which in this study refers to patches of grassland left unplanted within a commercial timber production landscape, will be referred to as remnant grassland patches (RGPs). The term "ecological networks" as used to refer to the interaction between species within food web ecology, taking the form of flower-visitor networks in this study, will be referred to as flower visitation networks (FVNs).

Pollination is vital for much of the planet's biodiversity (Kearns et al., 1998; Bascompte & Jordano, 2007). Therefore, pollinators, their population dynamics and the systems within which they interact should be prioritised for research within conservation, and for the sustainable use of biodiversity in both natural and agricultural and ecosystems (Eardley, 2001; Kehinde & Samways, 2014a). Increasingly, the community scale of pollination processes is being addressed by applying interaction network approaches to plant–pollinator communities (Baldock et al., 2011). The use of interaction networks, particularly those with beneficial interaction such as plant-pollinator networks, has been identified as crucial to conservation (Vázquez et al., 2009; Burkle & Alarcón, 2011; Kehinde & Samways, 2014b). This ecosystem

approach allows for the quantification of interactions within and between trophic levels, allowing examination of issues such as species coexistence and the consequences of species addition or loss (Memmott & Waser, 2002; Traveset & Richardson, 2006; Bascompte & Jordano, 2007; Lopezaraiza-Mikel et al., 2007). An understanding of the pollination systems of plant species, especially those within fragmented landscapes, is likely to provide important insights for their conservation (Carvalheiro et al., 2008). Thus, flower visitation networks were chosen as an analysis method for the purpose of this study, to investigate how interaction networks of grassland ecosystems are affected by anthropogenic change.

South Africa's grassland biome

The grassland biome of South Africa is a biodiversity hub, with extremely high species diversity relative to its size. The biome covers approximately 16.5% of the country's surface, and provides a home for approximately 50% of South Africa's endemic mammals, just over 30% of the country's endangered butterflies, approximately 75% of its threatened avian species, and is a global hotspot for plant diversity (Lombard, 1995; Cowling & Hilton-Taylor, 1997; Reyers & Tosh, 2003; Neke & du Plessis, 2004). Grasslands also provide many important ecosystem services (Reyers et al., 2001; Samways et al., 2010). Grasslands sequester carbon, removing it from the atmosphere and storing it in the soil, thereby mitigating climate change (Burke et al., 1989; Sala & Paruelo, 1997). Grasslands also protect against flooding and erosion by reducing runoff, storing excess water in wetlands or underground, creating a water supply (Kotze & Morris, 2001). In South Africa, many plants used for traditional medicines are found in grasslands, and worldwide, communities use grasslands for hunting, collecting fruit and thatch grass (Sala & Paruelo, 1997; Friday et al., 1999; Williams et al., 2000; Dzerefos & Witkowski, 2004). More than half of South Africa's grassland biome is transformed. The majority of the remaining natural areas are used as grazing for livestock, and only 1.6-2% of the biome is formally protected (Fairbanks et al., 2000; Neke & du Plessis, 2004; O'Connor, 2005). The grasslands of South Africa have also been greatly impacted by the invasion of alien vegetation due to inappropriate management and suppression of fire regimes (Bredenkamp et al., 2002; Lipsey & Hockey, 2010).

Study area

The Midlands region of the KwaZulu-Natal consists of a matrix of Midlands Mistbelt Grassland, Southern KwaZulu-Natal Moist Grassland and Drakensberg Foothill Moist Grassland (Mucina et al., 2005). Although these vegetation types are structurally quite similar,

they differ in their grass species composition, and additionally, occur on different soil types (Mucina et al., 2006). Midlands Mistbelt Grassland soils have wet soil dominated by mostly shale, but also some sandstone, while Drakensberg Foothill Moist Grasslands are found on drier soils which are dominated by sandstone and mudstone (Mucina & Rutherford, 2006). These soils are favourable for crop production, being relatively deep, highly leached and quite acidic (Manson, 1996). The Drakensberg foothill moist grassland of South Africa is of primary conservation concern (Wakelin & Hill, 2007; South African Forestry Magazine, 2011). The study site also forms part of the Maputaland-Pondoland-Albany biodiversity hotspot recognised due to its high plant endemism (Perera et al., 2011). Afforestation is of particular threat to South African grasslands, particularly the Maputaland-Pondoland-Albany biodiversity hotspot, because much of the area with the highest levels of biodiversity largely overlap with the most suitable areas for commercial timber plantations (Allan et al., 1997; Neke & du Plessis, 2004). By 2004, about 3.3% of South Africa's grasslands had already been cleared and planted with alien eucalyptus and pine trees (Neke & du Plessis, 2004), a number which may now have increased.

As the demand for timber continues to increase globally, so more areas of the world will be converted to commercial timber plantations (Cubbage et al., 2010; Pryke & Samways, 2012a). The continued growth of plantation forestry is a risk to global biodiversity as the plantations themselves contribute little to biodiversity (Pryke & Samways, 2009; Bremer & Farley, 2010). Remnant patches within commercial forestry plantations have been shown to help mitigate compositional biodiversity loss (Pryke & Samways, 2012b), however, few studies have examined the functional diversity retained in these areas.

Problem statement and research question

In conservation ecology it is not only necessary to set aside areas for conservation, but it is also extremely important to make sure that these areas are diverse and ecologically complex. The complexity of an ecosystem, referring to the number of species, their interactions, interaction strengths, and the evenness of the species in the system, affects its stability (Pimm, 1984). The stability of an ecosystem reflects aspects of its persistence, resilience, resistance and robustness; it is the ecosystems ability to return to its original state after perturbations, and the speed at which this can happen (Pimm, 1984; Dunne et al., 2005). The more complex an ecosystem is, the more stable it has been found to be (Van Voris et al., 1980). Therefore, maintaining stable ecosystems is vital for the conservation of biodiversity and the maintenance

of ecosystem services in South Africa, and all over the world, due to the large amount of disturbance inflicted on natural systems. In South Africa, forestry has replaced large areas of natural grassland. Although up to one third of the commercial forestry plantations are left unplanted, it is not known how effective these areas are in conserving functional biodiversity, given the influence of the alien species planted for forestry that surround them. Complicating this matter further is that exotic species such as *R. cuneifolius* is invading large sections of the natural grassland areas that have been set aside for conservation in these RGPs. To ascertain the level of conservation value and level of biodiversity of RGPs in the context of surrounding forestry and invasive bramble, this project examines the FVNs of these areas, as well as PAs, where bramble is present and where bramble is absent. By knowing how, and to what extent, the conservation value of grasslands within RGPs is affected, management practices can be put into place to maximise conservation of biodiversity.

The presence of *Rubus cuneifolius* may affect the biodiversity of natural grasslands in a negative way through competition for pollinators with native species, but brambles might well facilitate the pollination of grassland species. At the landscape level, RGPs may have reduced biodiversity when compared to PAs because of their context (being surrounded by alien species) or because of their size and relative isolation. It is critical to learn how these factors affect grassland ecosystems so that landowners may know how to manage these areas for maximum functional diversity, and therefore, conservation.

Thesis aims and structure

The overall aim of this thesis is to determine how well the RGPs conserve pollination functional diversity compared to a local PA, and how this is affected by the presence of an invasive alien plant. This project has two research chapters:

The aim of chapter 2 is to determine how the conservation value of grassland ecosystems is affected by the fragmentation caused by commercial timber plantations and the invasive alien plant *Rubus cuneifolius*. This will be done by evaluating compositional changes in flower-visitation and flower-visitor diversity, as well as flower diversity and abundance of naturally occurring grassland plants, within the following:

- Protected areas, in the absence of *Rubus cuneifolius.*
- Remnant grassland patches within forestry plantations, in the absence of *Rubus cuneifolius.*

- Protected areas, in the presence of *Rubus cuneifolius.*
- Remnant grassland patches within forestry plantations, in the presence of *Rubus cuneifolius*

In chapter 3, I will ascertain how the complexity, stability and robustness of interaction networks of grassland ecosystems are affected by commercial timber plantations and the invasive alien plant *Rubus cuneifolius*. This will be done by evaluating flower visitation networks of naturally occurring grassland plants:

- Within protected areas, in the absence of *Rubus cuneifolius.*
- Within remnant grassland patches within forestry plantations, in the absence of *Rubus cuneifolius.*
- Within protected areas, in the presence of *Rubus cuneifolius.*
- Within remnant grassland patches within forestry plantations, in the presence of *Rubus cuneifolius.*

From these objectives I should be able to determine how RGPs in transformed landscapes and invasion by *R. cuneifolius*, separately and together, affect the functional diversity value of grasslands, as well as the complexity, stability, and robustness that these pollination networks experience in response to change. The outcomes of this study will allow me to compare the four different types of sites to determine the impact of both *Rubus cuneifolius* and commercial timber plantations on flower visitation of natural grassland plant species (Chapter 4). I will therefore be able to determine how effective RGPs are in mitigating impacts of afforestation as compared to PAs, in respect to their conservation and biodiversity value, and how best to manage them (Chapter 4). This will allow me to set out management goals for these areas to maximise functional biodiversity conservation.

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CHAPTER 2

Compositional changes in flower visitation and flower species of a landscape transformed by commercial timber plantations, and the invasion of *Rubus cuneifolius*.

Globally, the increasing human population is leading to landscape transformation and fragmentation, and threatening biodiversity. Alien species invasions add to this global biodiversity crisis. The species-rich and diverse grasslands biome of South Africa is an important centre for plant endemism that provides vital ecosystem services such as water filtration and storage. However, much of this biome is transformed, particularly by commercial forestry plantations. Much of the remaining untransformed areas are restricted to remnant grassland patches (RGPs) within forestry areas. These were established to aid biodiversity conservation. However, invasive alien plant species also thrive in these landscapes, and there is limited information on their impact on native biodiversity. This study examined the effect of the invasive alien weed *Rubus cuneifolius* on flower visitation in remnant fragments of natural grasslands within timber plantations, and protected areas of natural grasslands in South Africa. Flower visitation surveys were conducted over 30 sites. Contrary to expectations, flower abundance of native plant species was higher within remnant grassland patches within timber plantations than in protected areas. However, this only occurred in the absence of *R. cuneifolius*. The presence of bramble also had a significant negative effect on the flower-visitor assemblage composition, as did location of the site (whether it was within a protected area or the remnant area). However, uninvaded RGP and PA sites displayed similar flower-visitor assemblages. Invaded PA and RGP sites had different assemblages than uninvaded sites, but also different assemblages from each other, and both displaying loss of specialist flower-visitor species. This suggests that RGPs do function to conserve some biodiversity, but that invasive brambles greatly reduce the effectiveness of RGPs, and should be eradicated.

Introduction

Increasing anthropogenic disturbance resulting in habitat loss and fragmentation is a serious threat to biodiversity (Ewers & Didham, 2006; Filgueiras et al., 2011). Habitat transformation leads to fragmentation and isolation of populations, which can lead to the breakdown of metapopulations (Hanski, 1998). Invasions by alien plant species add to this global threat to biodiversity and ecosystem functioning (Mack et al., 2000; Pimentel et al., 2001; Gurevitch & Padilla, 2004) and are making conservation management increasingly difficult. These threats to biodiversity are increasingly detrimental in areas with exceptionally high indigenous species richness and diversity (Myers et al., 2000).

The grassland biome of South Africa is a rich and diverse centre of plant endemism, and also contains half of the country's endemic mammal species, a third of its endangered butterfly species, and provides habitat for most of South Africa's threatened bird species (Lombard, 1995; Cowling & Hilton-Taylor, 1997; Reyers & Tosh, 2003). Much of South Africa's water

originates in the grasslands biome, where intact ecosystems reduce runoff, thereby reducing erosion and storing excess water (Kotze & Morris, 2001). Despite its role in ensuring the quality and quantity of water at larger scales, the grassland biome is heavily degraded. Approximately a third of the biome has already been irreversibly transformed through commercial forestry, urban development and agriculture, with only 1.6% under formal protection (Neke & du Plessis, 2004; NGBP, 2007).

Globally, commercial forestry is rapidly expanding, and is a well-known threat to biodiversity (Rouget et al., 2003; Brokerhoff et al., 2008). Afforestation is of particular threat to South African grasslands because the areas of grassland with the highest levels of biodiversity largely overlap with areas that are most suitable for commercial timber plantations (Allan et al., 1997; Neke & du Plessis, 2004). To ameliorate the fragmentation of natural vegetation caused by forestry, commercial timber production companies implement matrixes of remnant habitat patches. These remnant patches, which are common features in South African forestry production landscapes, are strips or patches of remnant habitat which connect protected areas and other natural areas to each other within transformed landscapes (Jongman, 1995; Samways et al., 2010). Remnant areas aim to minimise the effects of fragmentation of natural areas in managed landscapes (Jongman, 1995; Beier & Noss, 1998). To ensure added complexity, these networks often also contain nodes that include particular landscape features or ecosystems such as hilltops, natural forest patches or wetlands. Although helpful in alleviating fragmentation, these remnant patches can often contain impoverished faunas compared to larger areas of grassland (Weibull et al., 2003). The fragments can be compared to oceanic islands surrounded by hostile altered habitat (Diamond, 1975). The isolation of patches leads to slower immigration by new species, and slower repopulation after local extinctions (Simberloff, 1974). In addition, commercial forestry plantations may negatively affect processes such as pollination in these patches, which could lead to considerable economic and ecological consequences (Tscharntke et al., 2005; Gallai et al., 2009). The problem of fragmentation is compounded by the invasion of many of the natural remnant habitats by alien species. The invasion of alien plant species has been established as one of the greatest threats to biodiversity and community structure world-wide (Elton, 1958; Wilcove et al., 1998; Mack et al., 2000).

American bramble (*Rubus cuneifolius*) is considered one of the most serious invasive plant species in the Mistbelt region of the KwaZulu-Natal. Environmental conditions in the area, as well as the lack of natural enemies and competitors, have enabled bramble to become a naturalised weed (Erasmus, 1984). Bramble represents a serious threat, particularly to specialist

grassland taxa, as its encroachment may lead to communities more characteristic of woodlands (Bredenkamp et al., 1996; Lipsey & Hockey, 2010). This species infests large areas with thorny, dense stands, and it spreads rapidly due to its efficient reproductive system (Erasmus, 1984). The establishment of this species causes several problems. Infestations in natural vegetation limit accessibility to grazers, ultimately suppressing vegetation production and livestock carrying capacity (Erasmus, 1984). Despite its detrimental and widespread effects in areas in which bramble has become naturalised, very little information is available on its effects on native biodiversity and ecological processes within production landscapes.

The decline of pollinators, which are key in ecosystems, is likely to negatively impact ecosystem functioning and may even lead to economic damage (Costanza et al., 1997; Kearns et al., 1998). Interactions between plants can have both positive and negative consequences for flower-visitors. This is because species can support, attract or share pollinators (Real, 1983). In natural systems, there should be balance between these factors to ensure successful pollination, but invasive flowering plants can have profound effects on these communities. There have been a number of studies on competition for pollinators between invasive alien and naturally-occurring species. Invasive species can affect both pollinators and pollinated plants by disrupting ecosystems. When pollinators visit invasive species, they can be drawn away from native plant species, resulting in reduced reproductive capacity of native plants (Chittka & Schurkens, 2001; Brown et al., 2002). Invasive species can have a diluting effect on the pollen of native species by flooding the ecosystem with their own pollen in large amounts (Larson et al., 2006). Invasive species can also affect pollination indirectly by competing with native species for resources (Davis et al., 2000; Brooks, 2000). However, in contrast, it is also possible for invasive species to facilitate the pollination of native species by attracting more pollinators to the area (Morales & Traveset, 2009).

To understand how best to manage biodiversity for maximum conservation potential, there is a need to determine the value of RGPs within commercial forestry plantations while considering the added complication of the invasive weed *R. cuneifolius*, and the interactive effects of these two factors (location and bramble). Therefore, this study tests the following three hypotheses:

(i) Natural flower abundance and diversity of native plants are reduced by alien infestation and fragmentation.

(ii) Flower assemblages and flower-visitor assemblages of native grassland species are negatively affected by alien infestation (in this study, the presence of bramble, *R.*

cuneifolius), and fragmentation (i.e. here measured via location (protected areas (PAs) or remnant grassland patches (RGPs)) within the forestry plantations).

(iii) The number of visits to native flowers, and the diversity of flower-visitors are reduced by alien infestation and fragmentation.

Methods

Site selection

The Midlands of KwaZulu-Natal ranges in elevation from 1400 to 1800 m above sea-level and receives high annual rainfall (800–1280 mm), most of which falls during the summer months (Sandwith, 2002; Mkhabela & Materechera, 2003). Temperatures range between 2°C and 38.8°C, with a mean annual temperature of 14.1°C (Mkhabela & Materechera, 2003; Wakelin & Hill, 2007). This region consists of a matrix of Midlands Mistbelt Grassland, Southern KwaZulu-Natal Moist Grassland and Drakensberg Foothill Moist Grassland (Mucina et al., 2005). Although structurally quite similar, these grassland types differ in their grass species composition and also occur on different soil types (Mucina et al., 2006). Midlands Mistbelt Grassland have wet soil dominated by shale and some sandstone, while Drakensberg Foothill Moist Grasslands are on drier soils dominated by sandstone and mudstone (Mucina & Rutherford, 2006). These soils are favourable for crop production, being relatively deep, highly leached and quite acidic (Manson, 1996). Commercial timber plantations of alien trees are the most abundant form of land transformation in the area (Kirkman & Pott, 2002).

This study was conducted in the commercial timber plantation Gilboa Estate (29°25′S 30°30′E) and the adjacent protected area (PA), Mount Gilboa Nature Reserve, in the Karkloof area of the KwaZulu–Natal Midlands. This plantation covers an area of approximately 52.4 km^2, just over a third of which is designated for conservation (Lipsey & Hockey, 2010) in compliance with The Department of Water Affairs and Forestry (DWAF; now separated into the Department of Water Affairs and Sanitation and the Department of Agriculture, Forestry and Fisheries) and Forestry Stewardship Council (FSC) recommendations (Jackelman et al., 2006). In total, these remnant patches comprise an extensive 5 000 km^2 of semi-natural- grassland and indigenous forest within 18 000 km^2 of commercial timber plantations in South Africa and can potentially provide opportunities for conservation (Kirkman & Pott, 2002; Samways, 2007a). Gilboa's open patches consist largely of firebreaks, riparian zones, roads, and areas below power lines, as is common for remnant patches. However, there is a large continuous patch of grassland on Gilboa which is interconnected with the rest of the RGPs, the Mount Gilboa

Nature Reserve (Lipsey & Hockey, 2010). This private nature reserve was officially proclaimed under the National Environment Management Protected Areas Act in 2010, and was the first nature reserve to be set aside within commercial forestry land as part of the biodiversity stewardship programme (South African Forestry Magazine, 2010; 2011**).** Mt Gilboa is important for hydrology as it contains three important river systems, key wetlands and several types of grassland vegetation. Combined with its connectivity to the Karkloof Nature Reserve, this makes it an extremely valuable asset to biodiversity conservation of South African grasslands (South African Forestry Magazine, 2011). However, the presence of the invasive bramble (*R. cuneifolius*) is an environmental concern in both RGPs and the protected areas.

Sample design and data collection

Within this commercial timber plantation region, I focused on four landscape contexts: 1) protected area without bramble (PA.absent), 2) RGPs without bramble (RGP.absent), 3) protected areas with invaded by bramble (PA.present) and 4) RGPs invaded by *R. cuneifolius* (RGP.present). Ten sites (see Fig. 1) were chosen in each of the PA.absent and RGP.absent categories, and five each for PA.present and RGP.present. Fewer bramble invaded sites were sampled due to difficulty in finding flowering bramble. All sites had a minimum distance of 300 m between sites of the same type in order to minimise the chances of sampling the same individual flower-visitor, and RGP sites were chosen within RGPs that were between 50 and 200 m wide only, in order to standardise patch size.

Plant communities

Ten focal plant species were identified in order to make flower-visitor observations manageable. These species were the most frequently encountered native flower species found flowering within the sampling area. These species were (in order of abundance): 1) *Helichrysum pallidum* (Boleba), 2) *Helichrysum cymosum* (Yellow-tipped straw-flower); 3) *Senecio bupleuroides* (Yellow Starwort); 4) *Senecio tamoides* (Canary Creeper); 5) *Acalypha peduncularis* (Brooms and Brushes); 6) *Pentanisia prunelloides* (Wild Verbena); 7) *Eriosema squarrosum*; 8) *Senecio elegans* (Wild Cineraria); 9) *Lobelia flaccida*; 10) *Hypoxis hemerocallidea* (African Potato) (Fig. 2).

At each site, a 2 x 2 m quadrat was erected. These quadrats were placed in such a way that they maximised the number of representative focal species. Within each quadrat, all focal plant species were counted and identified (as a measure of flower diversity). When *R. cuneifolius*

was present at a site, quadrats were placed within 1 m of the bramble patch, while at bramble absent sites quadrats were laid out randomly. In addition, flower abundance (the total number of flowers of all focal species for that plot) was also determined. For the purposes of this study a "flower" is defined as a floral unit, including both flowers and pseudanthia. A pseudanthium is an inflorescence of anything from a small cluster of flowers to hundreds or thousands of flowers grouped together to form a single flower-like structure (Eames, 1961).

Flower-visitor observations

Observations were carried out three times at each site between the periods of 12 November and 11 December 2013, and 15 January and 14 February 2014, during bramble flowering. These data were pooled for analyses. The exact location of each quadrat was not retained in each subsequent round, but set again to maximise focal flower-visit density within a few metres of the previous quadrat. Observations of flower-visitors were conducted by two observers, standing at opposite corners of each quadrat, whom recorded any flower-visitors to focal species for a period of 15 minutes. Flower-visitors to these focal species were identified by sight, and if this was not possible, visitors were captured for later identification. The observations of both observers were pooled. Visits were defined as a flower-visitor coming to rest on the centre of a flower. The reference specimens were then put into vials with alcohol, or pinned, and are stored at the Stellenbosch University Entomology Collection, Stellenbosch, South Africa (USEC). In order to ensure that data collection was unbiased, sampling was only carried out between 08:00 and 17:00 when cloud cover was below 50%, there was no rain and wind speed was below 10 m/s. At each quadrat, environmental- and site variables were measured including; a) time, b) date, c) distance to the closest plantation, d) elevation, e) maximum wind speed, f) cloud cover, g) humidity and h) temperature. Maximum wind speed, humidity and temperature were measured with a handheld anemometer (Testo 410-2).

Insect classification

The flower-visitors were not identified to the species level, but instead sorted into morphospecies as described in Gerlach et al. (2013). With the morphospecies approach, a reference collection is created of all new species encountered, and each is given a surrogate name. The key to this approach is that individuals of one species found in different samples will be assigned the same species name (morphospecies), allowing a researcher to study beta-diversity and compositional changes of flower-visitors across a study without having to wait for the species to be formally identified. Morphospecies were also sorted into higher taxonomic

levels for ease of analysis. These groupings were mostly Orders, with the exception of Apoidea (a superfamily within Hymenoptera) and Culicidae (a family within Diptera). This was done so that Apoidea (bees) could be differentiated from wasps, due to their importance as pollinators. Mosquitoes (Culicidae) were separated from Diptera so that the response of flies could be examined in more detail. The morphospecies groupings were as follows: A) Coleoptera; B) Apoidea (all bee species encountered); C) Hymenoptera (bees excluded); D) Diptera (excluding Culicidae), E) Hemiptera; F) Lepidoptera, G) Culicidae.

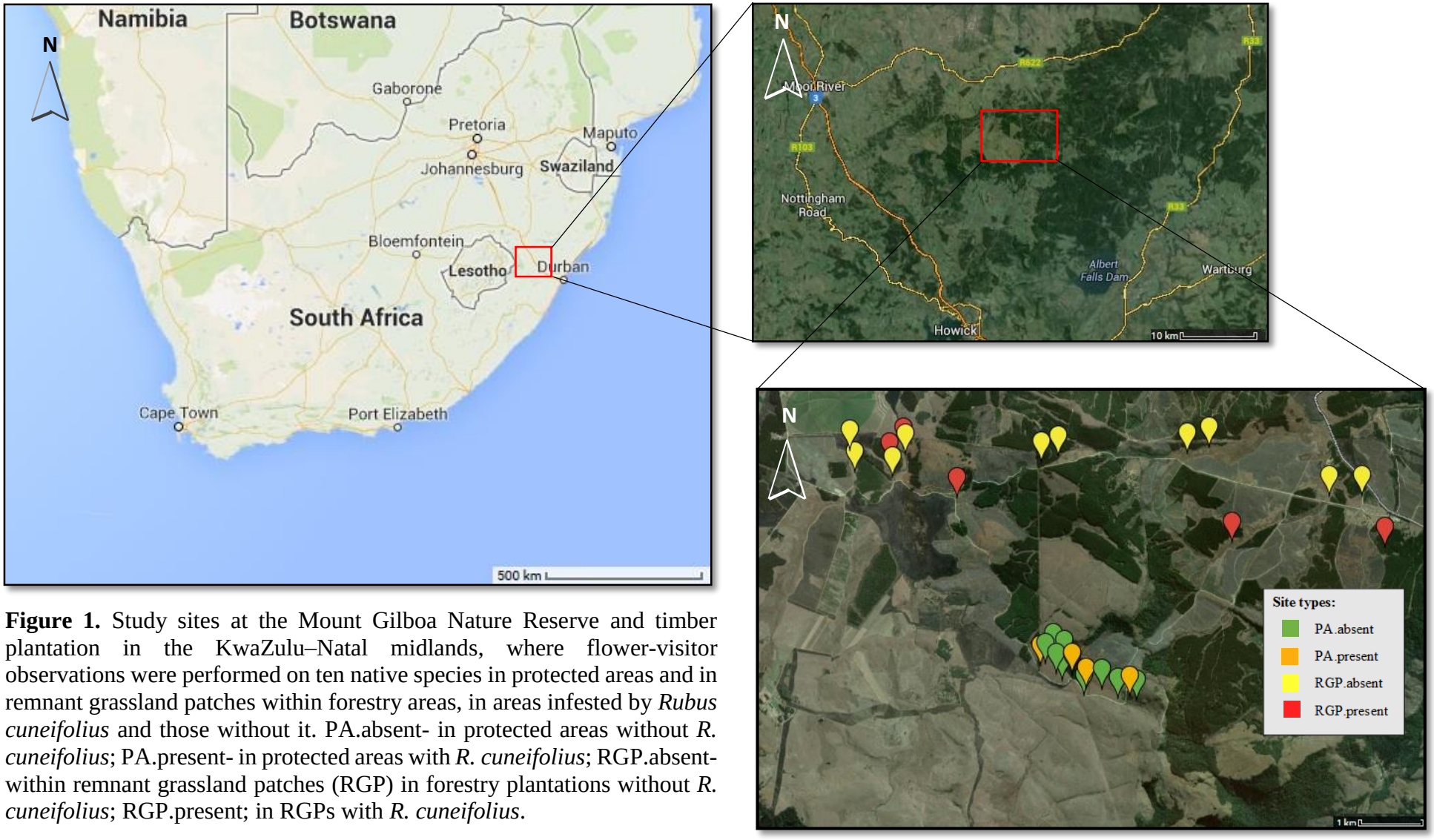


Figure 1. Study sites at the Mount Gilboa Nature Reserve and timber plantation in the KwaZulu–Natal midlands, where flower-visitor observations were performed on ten native species in protected areas and in remnant grassland patches within forestry areas, in areas infested by *Rubus cuneifolius* and those without it. PA.absent- in protected areas without *R. cuneifolius*; PA.present- in protected areas with *R. cuneifolius*; RGP.absent- within remnant grassland patches (RGP) in forestry plantations without *R. cuneifolius*; RGP.present; in RGPs with *R. cuneifolius*.

Figure 2. The ten focal plant species chosen for this study were: 1) *Helichrysum pallidum*, 2) *Helichrysum cymosum*; 3) *Senecio bupleuroides*; 4) *Senecio tamoides*; 5) *Acalypha peduncularis*; 6) *Pentanisia prunelloides*; 7) *Eriosema squarrosum*; 8) *Senecio elegans*; 9) *Lobelia flaccida*; 10) *Hypoxis hemerocallidea*. These were the most abundant flowering plant species in the study area. Picture 11 depicts *Rubus cuneifolius*.

Statistical analyses

Spatial autocorrelation

Within landscape ecology, scientists are becoming increasingly aware of the effects of spatial scale on biodiversity studies. Therefore, my data were tested for spatial autocorrelation by performing a Mantel test in the *ade4* package of the statistical software 'R' (R Development Core Team, 2007; Dray & Dufour, 2007).

Species accumulation estimate

Using the software PRIMER 6 (PRIMER-E, 2008), a Species-Accumulation Plot was constructed using flower-visitor data, with 9999 permutations, to ascertain whether sampling was sufficient. This was done using the non-parametric Chao2 index, as it is considered to be generally reliable (Hortal et al., 2006).

Flower species and flower-visitor assemblages in PAs and RGPs, with and without bramble

To determine the similarity of flower-visitor assemblages between sites, a PERMANOVA was performed using the add-on package PERMANOVA+ in PRIMER 6 (PRIMER-E, 2008). PERMANOVA cannot be used if the experimental design is unbalanced as it is sensitive to heterogeneous dispersions (Anderson & Walsh, 2013). Therefore, 5 sites were randomly removed from the site types RGP.absent and PA.absent, so that all treatments were only represented by five sites each. We also calculated an abundance based similarity index (Bray Curtis). Flower-visitor data were square root transformed to down-weight the influence of frequently recorded flower-visitors. A resemblance matrix was constructed using the Bray Curtis similarity measure. A PERMANOVA design was then created with location (RGP/PA) and bramble (present/absent) as fixed variables and the PERMANOVA then performed using the resemblance matrix. The site type data were further analysed using canonical analysis of principal coordinates (CAP), which is effective in delineating particular gradients of interest within a multivariate dataset despite the presence of other potentially important factors (Anderson & Willis, 2003; Anderson, 2008). The same procedure was carried out for focal plant species, to determine the flower assemblage for each site type. The data were also used to perform a SIMPER analysis, which calculates the similarity percentages of the species contributions.

Flower species diversity and abundance in PAs and RGPS with and without bramble

Generalized linear mixed effect models (GLMER) were performed in R using the *lme4* package (Bates & Sarkar, 2007). GLMER models were built to analyse the influence of location (PA/RGP) and presence or absence of bramble on flower abundance and flower diversity. Location, and presence or absence of bramble were included as fixed effects, as well as the interactive effects between the two, and average temperature was included as a random effect (McCulloch et al., 2008). These data were non-normal, thus a GLMER fit by a Laplace approximation with a Poisson distribution was used (Bolker et al., 2009). These analyses did not have overdispersion of variances compared to the models, thus a $\chi 2$ statistic and p–value were calculated (Bolker et al., 2009). Post-hoc analyses were performed on significant factors using a Tukey post hoc test in the R package *multcomp* (Hothorn et al., 2008).

Flower visits and flower-visitor diversity in PAs and RGPs with and without bramble

The same analysis as were done for flower species diversity and abundance were performed for number of flower visits and flower-visitor diversity. GLMERs were performed in order to analyse the influence of location (PA/RGP) and presence or absence of bramble on: number of visits to focal flower species, and flower-visitor diversity Location and presence or absence of bramble were included as fixed effects, as well as the interactive effects between the two, with average temperature included as a random effect. A GLMER Laplace approximation and a Poisson distribution were used as the data were non normal (Bolker et al., 2009). The analyses did not have overdispersion of variances, thus a $\chi 2$ statistic and p–value were calculated (Bolker et al., 2009), and post-hoc analyses were performed on significant factors using a Tukey post hoc test (Hothorn et al., 2008).

Results

Spatial autocorrelation

The data for flower abundance were spatially auto-correlated (Mantel test; $p = 0.009$), as was the number of visits to focal flowers by flower-visitors ($p = 0.003$).

Species accumulation estimate

Using the Chao2 index for cumulative species estimation over samples it was found that 131 flower-visitor species were encountered during the study, out of an estimated total of 150.93±8.96 flower-visitor species.

Flower species and flower-visitor assemblages in PAs and RGPs, with and without bramble

Flower species assemblages were not significantly different in species composition for any site type (Table 1), as shown in Fig. 3a. The focal flower species encountered the most in PA.absent sites were *H. cymosum* (44.95%), with *E. squarrosum* and *S. tamoides* not represented at all (Table 2). Almost half of the flowers encountered in RGP.absent sites were *H. pallidum* (46.23%), followed by *H. cymosum* (21.26%) (Table 2). Three of the focal species were not represented at all in RGP.absent sites type; *A. peduncularis*, *P. prunelloides* and *L. flaccida* (Table 2). Only seven of the ten focal plant species occurred in PA.present sites, and almost half of all flowers encountered were *H. pallidum* (Table 2: 47.06%). S. *tamoides*, *H. cymosum* and *E. squarrosum* were the second most encountered species in PA.present sites (Table 2: 18.14%, 18.10% and 18.10% respectively). Only five focal flower species were found in

RGP.present sites, and almost half of all flowers encountered were *H. cymosum* (45.91%). *S. bupleuroides* was the second most encountered focal flower species in RGP.present sites (Table 2).

When comparing the flower-visitor assemblages of all four site types, all had differences in their flower-visitor assemblages (Fig. 3b). However, the flower-visitor assemblages of uninvaded PA and RGP sites were similar (Fig. 3b). Sites with bramble present and bramble absent differed significantly (Table 1: F = 1.66, $p = 0.02$) with regards to their flower-visitor assemblages. Flower-visitor assemblages also differed significantly (Table 1: F = 2.04, $p < 0.01$) between sites in RGPs and in PAs. Also showing significant differences (Table 1: F = 1.76, $p = 0.01$), were the interactive effects of location and bramble on flower-visitor assemblages.

The most abundant group amongst flower-visitors at PA.absent sites were Coleoptera, comprising more than half of all flower-visitors (61.41%) (Table 3). Lepidoptera was the second-most represented order in PA.absent sites, with 16.08% (Table 3). Only two morphospecies comprised almost 50% of all flower-visitors to these sites, with the morphospecies COL005 (Coleoptera) a good indicator of PA.absent sites, representing 26.31% of all flower-visitors sampled here (Table 4). Flower-visitors to RGP.absent sites comprised mainly of morphospecies belonging to the orders Diptera (43.28%), Coleoptera (23.72%) and Apoidea (10.51%), with few morphospecies from the other orders (Table 3). Five morphospecies comprised nearly 50% of all flower-visitors encountered in RGP.absent sites, with the morphospecies HYM008 representing 16.85% of all flower-visitors to RGP.absent sites (Table 4). Visits to focal flower species within PA.present sites comprised mainly of Coleoptera (52.30%) and Diptera (26.44%), while Lepidoptera were barely represented (1.149%) (Table 3). Three morphospecies comprised over 50% of all flower-visitors in PA.present groups, with COL039 participating in 20.61% of all visits to this site type (Table 4). Flower-visitors to RGP.present sites comprised mostly of Coleoptera and Diptera (both with 36.03%), while no butterflies were sampled here (Table 3). Three morphospecies represented over half of all flower-visitors to RGP.present sites with DIP005 comprising 26.88% of all flower-visitors in this site-type (Table 4).

Table 1. F value and significance of the difference in flower species assemblage and flower-visitor assemblage as affected by bramble (present/absent) and location (RGP/PA), obtained by performing a PERMANOVA using Bray Curtis similarity.

	Source of Variation	**Pseudo-F**	***p***
Focal flower assemblage similarity	Location	1.28	0.304
	Bramble	0.61	0.649
	Location*Bramble	1.75	0.158
		Pseudo-F	***p***
Flower-visitor assemblage similarity	Location	2.04	0.002*
	Bramble	1.66	0.016*
	Location*Bramble	1.76	0.010*

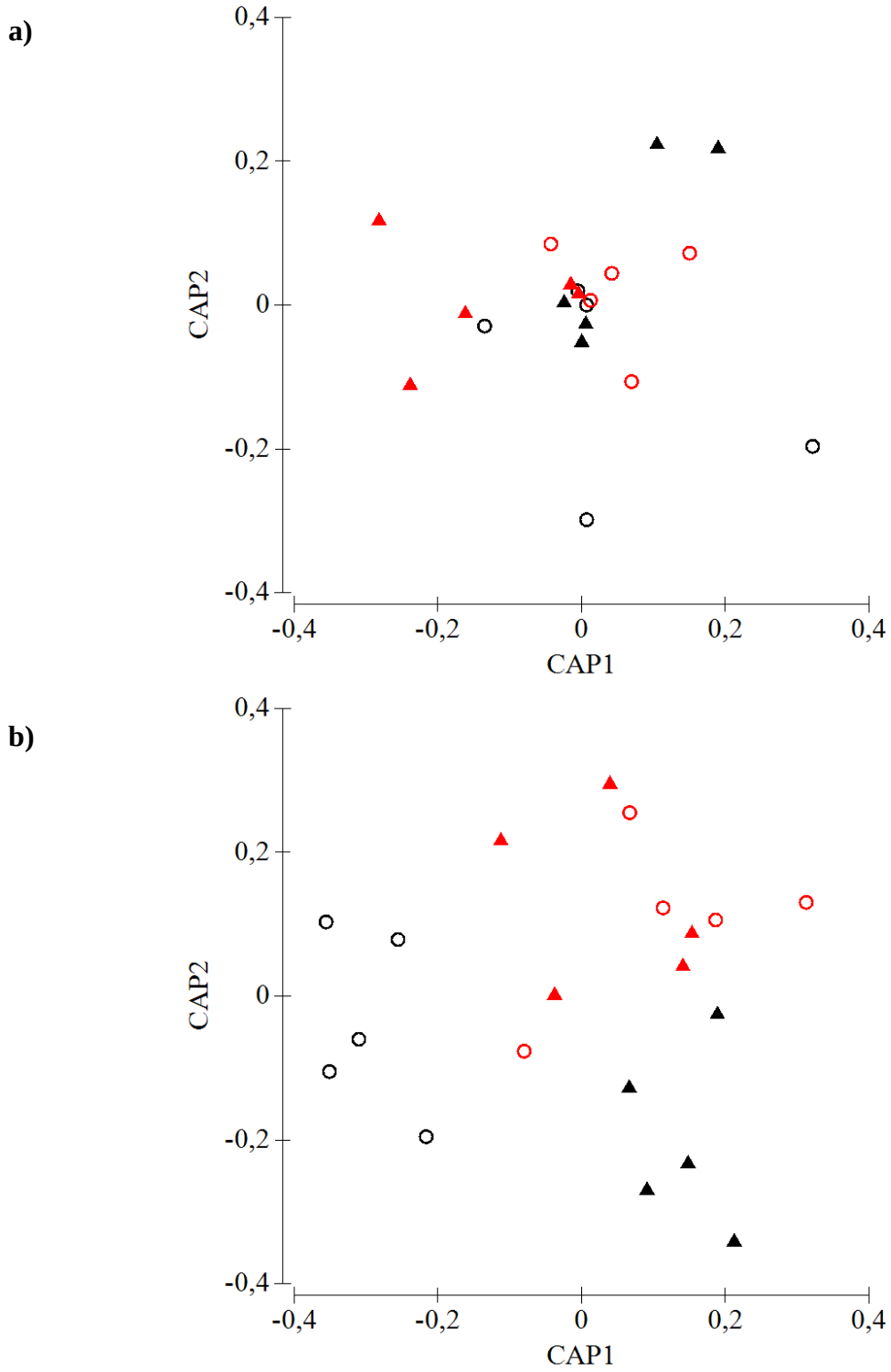


Figure 3. Canonical analysis of principal coordinates ordination using Bray Curtis similarity of the a) flower assemblage and b) flower-visitor assemblage for the site types: PA.absent vegetation type, sites in the protected area and without invasive bramble (red triangles), PA.present, sites in the protected area that are invaded by bramble (black triangles), RGP.absent, sites in the remnant grassland patches that are not invaded by bramble (red circles), RGP.present, sites in the remnant grassland patches that are invaded by alien *R. cuneifolius* (black circles).

Table 2. Percentage representation of focal plant species which the flower-visitors visited for each of the four site types; PA.absent- in protected areas without *Rubus cuneifolius*; RGP.absent- within remnant grassland patches (RGP) in forestry plantations without *R. cuneifolius*; PA.present- in protected areas with *R. cuneifolius*; RGP.present; in RGPs with *R. cuneifolius*.

	PA.absent	RGP.absent	PA.present	RGP.present	Overall
H. cymosum	23.6%	21.3%	18.1%	45.9%	**25.6%**
E. squarrosum	0%	3.63%	18.1%	0%	**1.55%**
S. bupleuroides	9.17%	11.5%	4.24%	25.3%	**12.2%**
S. tamoides	0%	15.8%	18.1%	3.62%	**10.2%**
L. flaccida	0.57%	0%	0%	0%	**0.14%**
P. prunelloides	14.4%	0%	0%	0%	**3.54%**
H. hemerocallidea	0.05%	0.18%	0%	0%	**0.09%**
A. peduncularis	7.30%	0%	11.27%	0%	**3.55%**
H. pallidum	44.9%	46.2%	47.06%	23.2%	**42.1%**
S. elegans	0%	1.39%	1.19%	1.94%	**1.11%**
	24.6%	**42.7%**	**15.6%**	**17.1%**	

Table 3. Percentage breakdown of visits by each morphospecies group for each of the four site types; PA.absent- in protected areas without *Rubus cuneifolius*; RGP.absent- within remnant grassland patches (RGP) in forestry plantations without *R. cuneifolius*; PA.present- in protected areas with *R. cuneifolius*; RGP.present; in RGPs with *R. cuneifolius*.

	PA.absent	RGP.absent	PA.present	RGP.present	Overall
Apoidea	2.89%	10.5%	2.98%	12.5%	**7.09%**
Coleoptera	61.4%	23.7%	52.3%	36.0%	**41.6%**
Culicidae	0.96%	3.18%	1.72%	2.21%	**2.14%**
Diptera	8.68%	43.3%	26.4%	36.0%	**29.0%**
Hemiptera	4.50%	7.33%	17.3%	3.68%	**5.53%**
Hymenoptera	5.47%	7.82%	11.5%	9.56%	**7.96%**
Lepidoptera	16.1%	4.16%	1.15%	0%	**6.70%**
	30.2%	**39.7%**	**16.9%**	**13.2%**	

Table 4. Percentage breakdown of the most abundant morphospecies for each site type; PA.absent- in protected areas without *Rubus cuneifolius*; RGP.absent- within remnant grassland patches (RGP) without *R. cuneifolius*; PA.present- in protected areas with *R. cuneifolius*; RGP.present; in RGPs with *R. cuneifolius*, determined by performing a SIMPER analysis. COL- beetles, APO- bees, LEP- butterflies, HYM- wasps, DIP- flies, HEM- bugs, CUL- mosquitoes.

PA.absent	**%**	**RGP.absent**	**%**	**PA.present**	**%**	**RGP.present**	**%**
COL005	26.3	HYM008	16.9	COL039	20.6	DIP005	26.9
COL011	20.9	COL011	10.3	COL005	18.5	COL014	16.2
LEP008	7.11	COL001	8.74	DIP009	12.6	COL003	8.49
HYM008	5.53	APO003	6.22	COL006	10.6	HYM006	7.53
COL003	4.90	DIP005	5.83	COL003	5.92	HYM007	7.26
COL006	4.89	DIP021	5.46	HYM008	4.39	COL018	7.01
COL002	4.11	HEM004	4.89	COL036	4.06	DIP015	3.13
COL018	2.85	DIP006	4.75	COL002	3.42	APO007	2.92
COL014	2.85	LEP008	3.64	DIP011	3.14	COL052	2.92
HYM005	2.28	DIP026	2.98	DIP020	2.93	HYM008	2.53
COL029	2.21	COL003	2.85	COL014	2.87	CUL001	2.30
COL012	2.21	COL002	2.63	DIP007	2.87	COL005	2.22
DIP006	2.12	COL045	2.46	-	-	COL022	2.22
COL028	1.05	HEM013	2.37	-	-	-	-
HEM008	0.93	DIP007	1.99	-	-	-	-
-		DIP009	1.97	-	-	-	-
-		DIP014	1.53	-	-	-	-
-		HEM008	1.24	-	-	-	-
-		CUL002	1.11	-	-	-	-
-		DIP002	1.00	-	-	-	-
-		HYM016	0.99	-	-	-	-
-		COL024	0.92	-	-	-	-

Flower species diversity and abundance in PAs and RGPS with and without bramble

Flower abundance was greatest in RGP.absent sites (Fig. 4a: mean = 667.3, stdev = 244.1), while PA.absent sites had the lowest flower abundance (mean = 385.1, stdev = 114.0). This difference was significant (Fig. 4a: $\chi^2 = 8.82$, $p < 0.001$). Flower abundance was significantly different for location ([PA/RGP] Table 5: $\chi^2 = 77.6$, $p < 0.001$), and the interaction between location and bramble ($\chi^2 = 2.03$, $p = 0.42$). Despite differences in flower abundance between the different sites, flower diversity did not differ significantly between the sites (Fig. 4b). Location, bramble, and the interaction between location and bramble had no effect on flower diversity (Table 5).

Figure 4. a) Average flower abundance and b) average flower diversity of sites for combined site types: PA.absent, PA.present, RGP.absent and RGP.present. Significance is indicated above each bar.

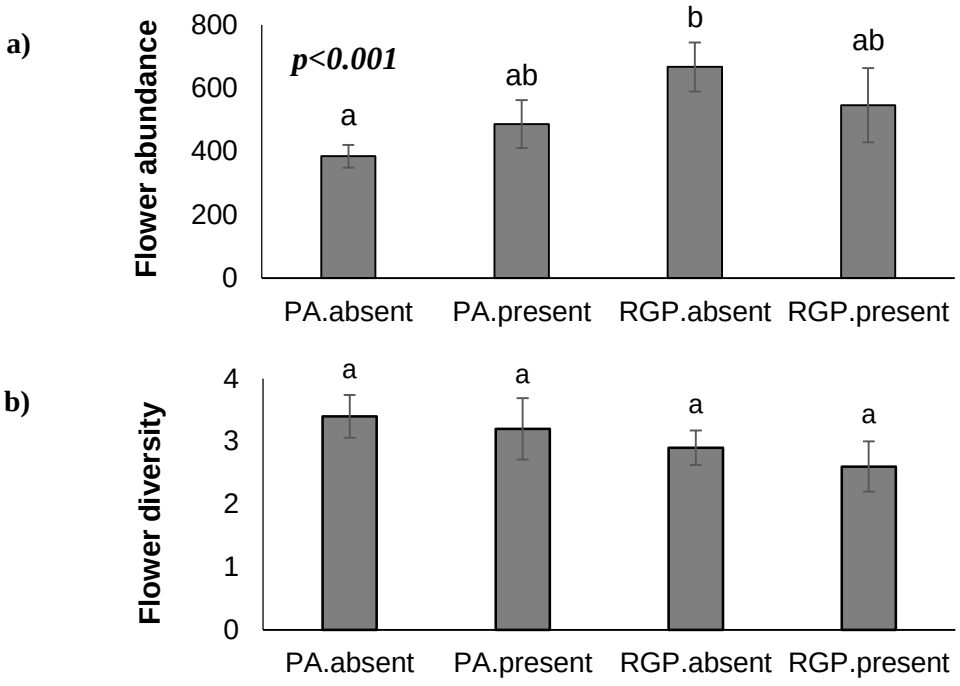


Table 5. The χ^2 value and significance in the difference of flower indices as affected by bramble (present/absent) and location (RGP/PA), obtained by performing generalized linear mixed effect models (GLMER).

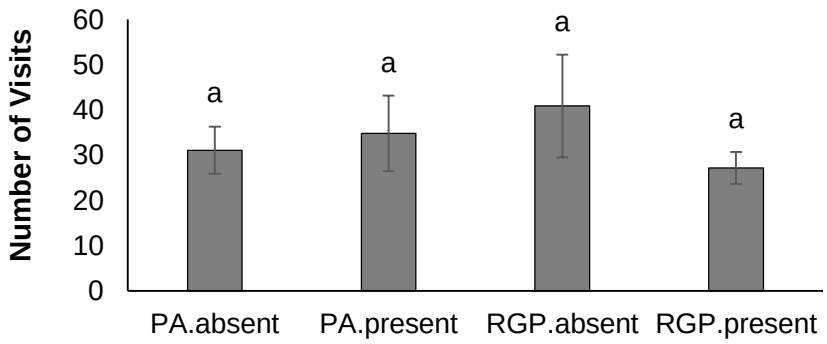
	Source of Variation	χ^2	***p***
Flower abundance	Location	77.6	<0.001*
	Bramble	0.07	0.789
	Location* Bramble	2.03	0.042*
		χ^2	***p***
Flower diversity	Location	0.14	0.711
	Bramble	0.70	0.404
	Location* Bramble	0.11	0.914

Flower visits and flower-visitor diversity in PAs and RGPs with and without bramble

The number of visits from flower-visitors did not vary significantly amongst the different sites (Fig. 5a). Number of visits to focal flower species was not significantly different for location or bramble, or for the interaction between bramble and location (Table 6). There were also no significant differences between flower-visitor diversity for any site type (Fig. 5b). Location, bramble, and the interaction between location and bramble had no significant effect on flower-visitor diversity (Table 6).

Figure 5. a) Average number of visits by flower-visitors and b) average flower-visitor diversity of sites for combined site types: PA.absent, PA.present, RGP.absent and RGP.present. Significance is indicated above each bar.

a)



b)

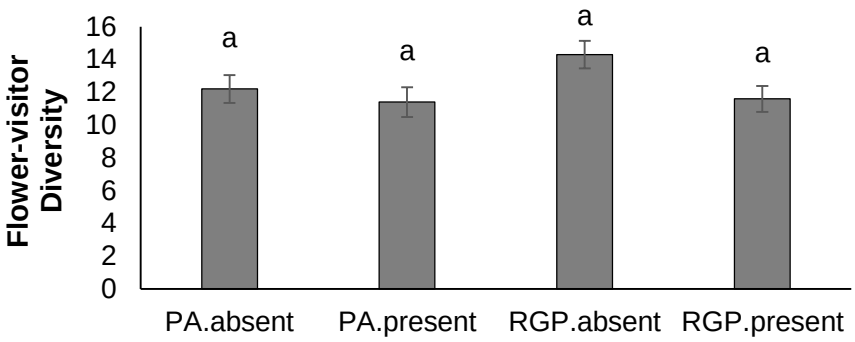


Table 6. Also shown is the χ^2 value and significance in the difference of number of visits to focal flowers and flower-visitor diversity, obtained by performing generalized linear mixed effect models (GLMER).

	Source of Variation	χ^2	***p***
Number of visits	Location	0.25	0.618
	Bramble	0.35	0.554
	Location*Bramble	0.28	0.779
		χ^2	***p***
Flower-visitor diversity	Location	1.64	0.201
	Bramble	1.27	0.259
	Location* Bramble	0.63	0.527

Discussion

Understanding the impact of multiple disturbances on biodiversity in transformed landscapes is extremely important for conservation. This is especially true when these disturbances are human-induced, and therefore manageable or even avoidable. In the face of increasing global demand for timber, and with decreasing natural forests, more of the world is being transformed for timber production (Cubbage et al., 2010). Commercial plantation forestry, especially with alien tree species, is a great risk to global biodiversity, as the plantations themselves contribute little to biodiversity (Armstrong & van Hensbergen, 1994; Pryke & Samways, 2009; Bremer & Farley, 2010). One way to soften the effect of land transformation on the functionality of a transformed area is to minimise fragmentation by leaving remnant grassland patches within commercial forestry plantations, essentially creating webs of small nature reserves. Unfortunately, these plantations and natural areas are often invaded by invasive plant species, causing further degradation in the landscape.

Due to the fact that all sites within the protected area were clustered, with the RGP sites spread throughout the entire forestry plantation, it was suspected that there could be a geographic bias in the analyses. This was confirmed when spatial autocorrelation was detected for flower abundance and the number of visits to focal flowers by flower-visitors. This limits the conclusions that can be drawn from these results, as any significant differences in those factors could be simply attributed to geographic position and not to the landscape management of the site.

This study found that flower abundance differed significantly between site types, with higher flower abundance in RGPs. Flower diversity, flower-visitor abundance and flower-visitor diversity did not differ significantly between site types. Despite these results, the assemblage composition differed significantly for anthophiles (flower visiting insects), although flower assemblages did not. Therefore; (i) the composition of insect assemblages is more sensitive to habitat change than the composition of plant assemblages, and (ii) measuring species diversity and abundance alone may not detect changes in insect assemblages. This is in agreement with Samways (2007b) who found that land transformation was particularly disruptive to insect assemblages, particularly to specialist species. With regards to the effects of location and bramble, or the interaction of the two, on species composition, this study found that the native flower assemblages were not significantly different between the different site types.

It is possible that the variability in the flower measurements of the 10 focal flower species lead to a bias in the results. The sampling method regarded flower and pseudanthia equally, however a pseudanthium of *Helichrysum cymosum* can support the visit of multiple flower-visitors, while a flower of *Lobelia flaccida* can support only one. Similar examples can be given for other flower-visitor species.

The flower-visitor assemblages were significantly different between the different types of sites, indicating a difference in species composition. The flower-visitor assemblages were affected by both location (RGP or PA) and bramble (whether it was absent or present), and also by the interaction of the two factors. However, uninvaded PAs and RGPs had similar flower-visitor assemblages. The significant effect of location indicate that these areas are affected by the fragmentation caused by commercial forestry plantation. The difference in assemblages could also, in part, be attributed to the clustered nature of all PA sites as opposed to RGP sites which were scattered throughout the plantation. Examples of similar studies in remnant patches of transformed landscapes had varied results. Pryke and Samways (2012a), who looked at conservation of natural forests in a forestry mosaic, found that there was a distinct grassland edge zone adjacent to plantation blocks, beyond which the effects of the plantation blocks were negligible. The main findings of Pryke and Samways (2012b), who sampled arthropods in remnant patches within commercial forestry plantations in KwaZulu-Natal, were that there were no significant differences in species richness or assemblage composition between PA and EN corridor interior zones. However, a study within the same local area as this study, by Bullock & Samways (2005), found that there was no significant difference in arthropod species assemblage composition across different sites, both inside the plantations and natural areas outside plantations. In many studies, it has been shown that corridors must be relatively undisturbed in order to allow movement (Hill, 1995; Haddad, 1999). This indicates that although commercial forestry does have an effect on the compositional diversity of grasslands areas within it (Pryke et al., 2013), the interior zones of RGPs are effective for conservation if they are kept in a near-pristine state and uninvaded.

The presence of alien bramble also significantly affected flower-visitor assemblages. American bramble is known to have a negative effect on the local biodiversity within the areas which it invades (van Wilgen et al., 2008). Invasive plants often influence the diversity of flower-visitors by causing some taxa to become very abundant, while reducing the abundance of others (Samways et al., 1996). Plant architecture is often more important in influencing flower-visiting insect assemblages than whether the plant is alien or indigenous (Samways & Moore,

1991). Factors such as the height and density of vegetation are important influencers of flower-visitor behaviour (Samways et al., 1996). Bramble is notorious for forming high, dense thickets which are extremely difficult to move through (Erasmus, 1984). This affects the assemblage of flower-visitors found in invaded areas. Floral traits have co-evolved with certain pollinator's dietary needs, mobility and ability to handle different types of flowers (Kevan & Baker, 1999; Vrdoljak, 2010) and are, therefore, important in determining the different responses of different groups of flower-visitors. This is another cause of the altered flower-visitor composition within invaded areas. Most alien plant species arrive in areas without their natural pollinators but thrive in the presence of generalist pollinators, with very few documented cases of alien plants failing to reproduce due to the absence of pollinators (Richardson et al., 2000). As generalist flower-visitors are more likely to visit alien plant species than specialists, it follows that invaded areas will have more generalist flower-visiting species than specialists, and therefore, a different species composition than uninvaded areas.

This study found that RGP.present sites had flower-visitors which were mostly flies and bees, as well as being the only site type to have no butterflies. PA.absent sites had few flies and bees, and many butterflies. RGP.absent sites were more reminiscent of PA.absent sites than RGP.present sites, with fewer flies and bees and many butterflies. PA.present sites had many bees and fly species, and one butterfly morphospecies. Diptera abundance has, in previous studies, been found to be increased by the presence of exotic vegetation (Breytenbach, 1986), indicating why more flies were found in invaded sites. Butterflies have long been used as ecological indicators of ecosystem health in many regions of the world and are known to be sensitive indicators of landscape change (Thomas, 1991; Oostermeijer & van Swaay, 1998). The absence of butterflies in RGP.present sites, and scarcity in PA.present sites, could indicate that these sites are indeed more degraded than uninvaded sites in the PA due to the commercial forestry plantations, invasive alien bramble, and an interactive effect between the two. When examining flower-visitor morphospecies for each site type, only 5.88% of morphospecies in RGP.present sites were unique to the site type, while a surprisingly high 32.5% of flower-visitor morphospecies in RGP.absent sites were only encountered in that site type. When looking at PA.absent sites, 26.6% of morphospecies were unique to the site type, while 17.9% of flower-visitor morphospecies were unique to PA.present sites. This strongly indicates that the invaded areas had a loss of specialist flower-visitor species and an increase in generalists, and that the interaction between location and bramble intensifies this effect.

Flower abundance of focal flower species in this study was not affected significantly by *R. cuneifolius*. Flower abundance was affected by location, as well as the interaction between bramble and location. Flower abundance was greatest in RGP.absent sites and lowest in PA.absent sites, seemingly indicating that commercial forestry plantations have a positive effect on flower abundance. However, since spatial autocorrelation was found for flower abundance, the increase in flower abundance is likely due to other factors such as increased nutrients in the soil or water availability in these areas. The presence of bramble reverses the effect of increased flower abundance, as in the presence of bramble, RGP sites no longer have significantly greater flower abundance than PA sites. This is due to competition for resources between the IAP and native flowering plant species. Invasive brambles are known to outcompete, and replace, indigenous plant species (Grenfell et al., 2005). This shows that the good conservation work done by implementing remnant grassland patches can easily and quickly be undone by alien vegetation and highlights the importance that *R. cuneifolius* be removed in these areas if positive conservation results are to be expected.

Flower diversity was not affected by bramble, location, or an interaction of the two effects. It is important to note that only the 10 most common native flowering species were surveyed in this study and the effects of fragmentation and invasion by bramble may be masked for more rare plant species. Although at first glance there seemed to be a trend towards a higher number of visits to focal flower species as well as higher flower-visitor diversity in RGP.absent sites than in any other site type, this was not significant. The number of visits to focal flower species was not significantly affected by *R. cuneifolius*, location, or an interaction of these factors. Flower-visitor diversity was also unaffected by bramble, location, and the interactive effects between bramble and location. This indicates that these remnant areas are effective with regards to mitigating the effects of land transformation and fragmentation, allowing most of the biodiversity within transformed landscapes to remain.

The results of this study have shown that RGPs are a vital conservation tool within transformed landscapes, which would otherwise support very little native biodiversity. Uninvaded RGPs and PAs display very similar flower-visitor assemblages. However, when there is invasion by *R. cuneifolius* within RGPs, these areas experience a loss of specialist flower-visitor species and subsequent replacement by more generalist species. This is in agreement with Pryke and Samways (2003) that the most important aspect of remnant patches is the habitat quality within them. A combination of factors involving the floral traits and plant-architecture of brambles

lead to different flower-visitors, and thus, altered flower-visitor assemblages in invaded areas. Therefore, the removal of *R. cuneifolius* within RGPs is crucial for their success in alleviating the effects of habitat transformation, specifically commercial forestry, on functionality of grasslands.

I show that remnant grassland patches within commercial forestry plantations successfully decrease the negative effects of land transformation on the flower visitation of the grasslands of the KwaZulu-Natal Midlands. However, these results stress the importance of keeping the RGPs clear of alien invasive plants, particularly *R. cuneifolius*. To improve the effectiveness of these RGPs for conservation and the resilience of this landscape to habitat transformation we also need to consider the functional aspects of biodiversity.

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CHAPTER 3

Flower-visitor interaction networks of a landscape transformed by commercial forestry and an alien invasive species.

No species on Earth lives in isolation, they each interact with other species and form complex networks. The structure of these networks is often affected by anthropogenic disturbance, which poses a significant threat to biodiversity worldwide. Due to the insufficient natural wood supply in South Africa, commercial forestry plantations are one of the dominant forms of landscape transformation in the country. Additional negative impacts on transformed landscapes include the problem of invasive alien plant species. *Rubus cuneifolius* (American bramble) is a major weed in South Africa, and is particularly problematic in and around commercial plantation blocks. Compounding this, is the global decline in pollinators, affecting ecosystems and impacting biodiversity. This study examines the effect of the invasive alien weed *R. cuneifolius* and fragmentation caused by landscape transformation on flower visitation networks (FVNs) in timber plantations and protected areas of natural grasslands in South Africa. By comparing FVNs in protected areas and RGPs, both invaded and uninvaded, this project will assess the negative impacts of the invasive species and landscape fragmentation on conservation value and biodiversity. Network-level analyses of flower visitation networks provide insight into the robustness of ecosystems in the face of biodiversity loss. Modularity was greatly reduced by the presence of bramble, indicating a reduction of complexity and organization. The mean number of shared partners of flowers-visitors and of focal flower species, connectance, nestedness and Shannon diversity were unaffected by presence of bramble and location. That ecological complexity, measured by modularity, of flower visitation networks differed between invaded and uninvaded areas, but not between PAs and RGPs, suggests that RGPs contribute to biodiversity conservation by promoting ecological complexity. However, invasive bramble reduces ecological complexity of both RGPs and PAs, and should be removed.

Introduction

Every species on Earth interacts with other species, either in neutral interactions, antagonistic interactions, or mutualistic interactions (such as predator-prey, and plant-pollinator interactions, respectively) (Tylianakis et al., 2010). These interactions form networks, the structure of which influences the resilience and robustness of the ecosystems that they occupy (Dunne et al., 2002a; Thébault & Fontaine, 2010). Until recently, the study of these networks has been largely ignored by conservationists in favour of a species composition approach. Many recent studies have, however, shown that anthropogenic disturbance results in not only habitat loss and fragmentation, which pose serious threats to conservation (Ewers & Didham, 2006; Filgueiras et al., 2011), but also affects the structure of interaction networks. This has consequences for ecosystem functions, such as pollination and seed dispersal (Thompson, 1994; Lopezaraiza-Mikel et al., 2007; Memmott et al., 2007; Aizen et al., 2008). It has been shown that drivers of global change may even alter network properties without causing biodiversity loss (Tylianakis et al., 2007; Laliberté & Tylianakis, 2010; Kehinde & Samways, 2014). It is therefore necessary for conservationists to assess how these interaction networks

are affected within areas affected by anthropogenic disturbance in order to determine the real damage that has been done.

Globally, pollinators are in decline, driven primarily by loss of natural environments through habitat modification (Winfree et al., 2009; Potts et al., 2010). Anthropogenic landscape transformation, such as the large-scale transformation of South Africa's natural areas for commercial forestry plantations (DWAF, 2006), is likely to affect plant-pollinator interaction networks, and therefore the reproductive success of plant communities (Hennig & Ghazoul, 2011). However, the extent to which species loss through land transformation affects ecosystems is thought to depend on the complexity of the ecosystem in question (Dunne et al., 2002b). Network-level analyses have experienced increased popularity in recent years for describing the robustness of systems towards perturbations (Bascompte & Jordano, 2007; Bascompte, 2010; Bahram et al., 2014).

In interaction networks, individuals, species, populations or habitats can be represented as nodes that are linked based on their biological interactions (Bahram et al., 2014). Within these networks, interactions can occur between different functional guilds or within the same guild, and are termed bipartite and unipartite networks, respectively (Bascompte & Jordano, 2007). Bipartite networks involve a minimum of two interacting functional guilds, and include parasitic, predatory and mutualistic relationships (Bahram et al., 2014). Early studies of mutualistic interactions only considered the presence or absence of an interaction between species, allowing for the identification of some general patterns to determine the functioning of the ecosystem in question (Memmot & Waser, 2002; Vázquez & Aizen, 2004; Bascompte et al., 2006; Olesen et al., 2007; Castro-Urgal et al., 2012). However, it soon became apparent to ecologists that the accuracy of these binary networks was limited. Thus, weighted measures, which describe the interaction strength between partners in mutualistic interactions, became necessary, thereby increasing the reliability of the network properties and facilitating their interpretation (Bersier et al., 2002; Blüthgen et al., 2006; Castro-Urgal et al., 2012). One of the simplest and also the most frequently used methods to weigh interaction strength in pollination networks is to include the number of pollinator visits to each plant species (Castro-Urgal et al., 2012; Chapter 2).

Some of the most commonly used indices for interaction networks are diversity, connectance, nestedness, and modularity (Thébault & Fontaine, 2010). The values of these network indices describe the number of species (diversity), the relative number of interactions (connectance),

the level of sharing of interaction partners among species (nestedness) and the degree of compartmentalization of the networks (modularity) (Thébault & Fontaine, 2010). These kinds of architectural patterns can provide complementary information on how interactions are organized in communities (Krause et al., 2003; Bascompte et al., 2006; Fortuna et al., 2010; Thébault & Fontaine, 2010), and how the communities function.

In addition to direct anthropogenic land transformation, invasion by alien plant species is also a global threat to biodiversity and ecosystem functioning (Mack et al., 2000; Pimentel et al., 2001; Gurevitch & Padilla, 2004). For example, American bramble (*Rubus cuneifolius*) is considered one of the most problematic invasive alien plant species in South Africa. Classified as widespread to abundant, it is particularly problematic within plantation areas and grasslands in South Africa (Le Maitre et al., 2002; Nel et al., 2004). Bramble replaces native plants, and impacts negatively on biodiversity (Reynolds & Symes, 2013). It is well known that invasive alien plants are able to influence essential ecosystem services such as pollination (Lopezaraiza-Mikel et al., 2007). Invasive flowering plant species can affect pollination of native flower species via competition (Chittka & Schurkens, 2001; Brown et al., 2002; Ghazoul, 2002; Larson et al., 2006) or facilitation (Moragues & Traveset, 2005). At a network level, alien species can potentially affect the whole interaction network, as many species are directly or indirectly connected to the alien species (Lopezaraiza-Mikel et al., 2007). This is because invasive species tend to be generalists, and tend to form links with generalist species within the networks they invade (Baker, 1965; Rejmanek & Richardson, 1996; Reichard & Hamilton, 1997). Thus, if we are able to assess how the networks of an ecosystem are being affected by anthropogenic change and alien invasive species, we can ascertain how these alien species are integrating into, and disrupting, local systems.

This study examines flower visitation networks, and their network indices, of native grassland plants within a landscape transformed by commercial timber plantation and invaded by *Rubus cuneifolius*. This is done in both a protected area, as well as within remnant grassland patches (RGPs) within the commercial forestry plantations. The purpose of this study is to determine how grasslands in these transformed landscapes are affected by both the presence of an invasive alien species, and fragmentation associated with forestry. Understanding how these factors affect flower visitation networks allows us to determine where management and planning efforts need to be concentrated in order to maximise conservation in forestry networks. The hypotheses tested in this study are that: (i) flower visitation networks are less complex and therefore less robust when in RGPs than in PAs, and also when invaded by *Rubus cuneifolius*;

(ii) the interactive effects of RGPs and invasion on network complexity will be synergistic, resulting in even less complex FVNs than expected in RGPs and invaded sites.

Methods

Site selection and sampling design

This study was conducted in the Karkloof area of the KwaZulu-Natal Midlands. The area consists of a matrix of Midlands Mistbelt Grassland, Southern KwaZulu Moist Grassland and Drakensberg Foothill Moist Grassland (Mucina et al., 2005, 2006). It is a summer-rainfall region with a mean annual temperature of 14.1°C (Sandwith, 2002; Mkhabela & Materechera, 2003; Wakelin & Hill, 2007). The dominant form of land transformation in this area is commercial forestry (Kirkman & Pott, 2002). Sampling was carried out at various sites across Gilboa Estate, a commercial timber plantation, as well as Mount Gilboa Nature Reserve, an adjacent protected area. The plantation covers an area of approximately 52.4 km^2, just over a third of which is unplanted as RGPs (Lipsey & Hockey, 2010). The nature reserve is very important for hydrology, containing three river systems, key wetlands, and several types of grassland vegetation (South African Forestry Magazine, 2011). The presence of invasive brambles (*Rubus cuneifolius*) is of environmental concern in both the RGPs and PA.

The sample design focused on four landscape contexts: i) protected area without *R. cuneifolius* (PA.absent), ii) RGPs without *R. cuneifolius* (RGP.absent), iii) PA invaded by *R. cuneifolius* (PA.present) and iv) RGPs invaded by *R. cuneifolius* (RGP.present). Ten sites (see Fig. 1) were chosen each for PA.absent and RGP.absent, and five each for PA.present and RGP.present. All sites had a minimum distance of 300 m between sites of the same type, and RGP sites were chosen only within RGPs between 50 and 200 m wide in order to standardise patch size.

Plant communities

Ten focal flowering species were used in this study. These species were (in order of abundance): 1) *Helichrysum pallidum* (Boleba), 2) *Helichrysum cymosum* (Yellow-tipped straw-flower); 3) *Senecio bupleuroides* (Yellow Starwort); 4) *Senecio tamoides* (Canary Creeper); 5) *Acalypha peduncularis* (Brooms and Brushes); 6) *Pentanisia prunelloides* (Wild Verbena); 7) *Eriosema squarrosum*; 8) *Senecio elegans* (Wild Cineraria); 9) *Lobelia flaccida*; 10) *Hypoxis hemerocallidea* (African Potato).

At each site, a 2 x 2 m quadrat was erected. When *R. cuneifolius* was present at a site, quadrats were placed immediately adjacent to the bramble patch, while at uninvaded sites, quadrats were laid out randomly. Flower abundance was also determined, using floral units as a measure (see Chapter 2).

Flower-visitor observations

Between the period of 12 November 2013 and 14 February 2014, three rounds of observation were carried out, whereby a 2 x 2 m quadrat was erected at each site within which all focal species were counted, identified and recorded. Any flower-visitors to the focal species were identified by sight or captured for identification. This was done for a 15 minute period at each site. For unbiased results, sampling was carried out only between 08:00 and 17:00, when cloud cover was below 50%, there was no rain and wind speed was below 10 m/s. At each site the following additional information was recorded; a) time, b) date, c) distance to the closest plantation, d) elevation, e) maximum wind speed, f) cloud cover, g) humidity and h) temperature.

Insect classification

Flower-visitors were identified to the morphospecies level, following Gerlach et al. (2013). Morphospecies were also sorted into higher taxonomic levels for ease of analysis. These groupings were mostly orders, with the exception of Apoidea (a superfamily within Hymenoptera) and Culicidae (a family within Diptera). This was done so that bees and flies could be studies in more detail due to their importance as pollinators. The morphospecies groupings were as follows: A) Coleoptera; B) Apoidea (all bee species); C) Hymenoptera (bees excluded); D) Diptera (excluding Culicidae), E) Hemiptera; F) Lepidoptera, G) Culicidae.

Statistical analyses

Using the Bipartite package in the R software (Dormann et al., 2008; R Development Core Team, 2007), flower visitation networks were constructed. First, a web was constructed with the focal flower species, the morphospecies groups observed visiting them, and their abundances for each landscape context (PA.absent, RGP.absent, PA.present and RGP.present). A graphical representation was then constructed with the *plotweb* function representing all 30 sites. Five FVNs were constructed, one representing all the interactions observed during data collection of the study, and one for all of the interactions in: 1) PA.absent, 2) RGP.Absent, 3) PA.Present and 4) RGP.Present.

Using *grouplevel* statistics in the Bipartite package of the software R, the mean number of shared partners for the lower level (focal flower species) were calculated for the overall interaction network and for each site (Dormann, 2011). Using *networklevel* statistics, connectance, weighted NODF (nestedness metric based on overlap and decreasing fill) and Shannon diversity were calculated for the overall FVN, each site type and each site. Weighted NODF was used as the measure of nestedness; it is a weighted nestedness index based on paired overlap in filled versus non-filled cells of matrices and decreasing marginal totals, and is a more consistent measure of nestedness (Almeida-Neto et al., 2008; Almeida-Neto & Ulrich, 2011; Wells et al., 2014). Modularity was calculated using the *computeModules* function in the Bipartite package of R for the overall FVN, as well as for each site (Dormann, 2011). Analyses at the network level are particularly useful for comparisons across different types of networks (Blüthgen et al., 2006).

In R, linear models were performed with one of the following indices as the response variable for each model: mean number of shared partners of focal flower species, connectance, weighted NODF, modularity and Shannon diversity. Location (whether the site was in a PA or RGP) and bramble (whether it was present or absent) were explanatory variables. Connectance, and other network indices are strongly dependent on network size (Goldwasser & Roughgarden, 1997; Blüthgen et al., 2006), and therefore, because more sites were sampled for uninvaded PA and RGP than invaded, 5 sites were removed at random from RGP.absent and PA.absent site types for these analyses. With the *multcomp* package, pairwise post-hoc Tukey tests were performed for each network- or group-level index by site type (Hothorn et al., 2008).

Results

Overall characteristics of flower visitation networks

The overall flower visitation network (Fig. 1) was diverse, with 114 morphospecies taking part in 1030 interactions over 30 sites. Coleoptera were the most common flower-visitors, participating in 41.6% of all interactions (47 morphospecies). Diptera were observed in 29% (27 morphospecies) of interactions, Hymenoptera, (excluding the superfamily Apoidea) took part in 8% (11 morphospecies) of interactions, Apoidea in 7.1% (7 morphospecies) and Lepidoptera participated in 6.7% (7 morphospecies) of total interactions. Hemiptera were observed in 5.5% (12 morphospecies) of visits, and Culicidae in 2.1% (3 morphospecies) of visits (Table 1). The number of focal flowers (defined as a floral unit, including both flowers and pseudanthia) observed in the overall flower visitation network were 15 634. Of these,

42.1% were *H. pallidum*, 25.6% were *H. cymosum*, 12.2% were *S. bupleuroides*, and 10.2% were *S. tamoides*. The remaining focal flower species had less than 5% representation each (Table 2). Within the overall FVN, it can be seen that Diptera had a large number of interactions with *Senecio bupleuroides* (Fig. 1).

The average flower abundance within PA.absent sites was 385.1 flowers per site. These consisted of 45.0% *H. pallidum*, 23.6% *H. cymosum*, and 14.4% *P. prunelloides*. Three of the focal flower species were not represented at these sites (Table 2). PA.absent sites had an average of 31.1 interactions per site, with a visits/flower ratio of 0.81:1. Sixty-four insect morphospecies took part in these interactions, with Coleoptera participating in 61.4% of these interactions (Table 1) and Lepidoptera in 16.1% of the interactions.

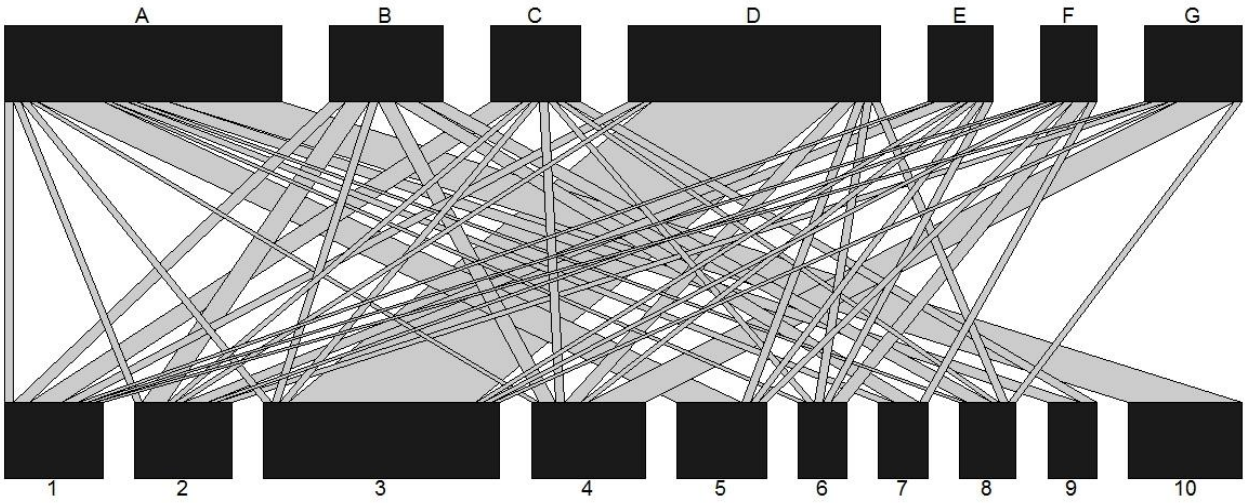
The average flower abundance observed within RGP.absent sites was 667.3 flowers per site. Of the flowers observed in these sites, 46.2% were *H. pallidum*, 21.3% were *H. cymosum*, and *S. tamoides* comprised 15.8%. Three focal flower species were not observed in this site type (Table. 2). RGP.absent sites had an average of 40.9 interactions per site, with a visits/flower ratio of 0.61:1. Eighty insect morphospecies were responsible for these interactions, with Diptera making up the majority (Table 1: 43.3%) of these interactions and Coleoptera in 23.7% of the interactions. The remaining interactions were from Apoidea, Hymenoptera, Hemiptera, Culicidae and Lepidoptera (Table 1).

There was an average flower abundance of 486.2 flowers per site. Of the 6 focal flowers species represented in this site type, 57.1% were *H. pallidum*, 18.1% were *S. tamoides*, and 18.1% were *H. cymosum* (Table 2). PA.present sites received an average of 34.8 visits per site, with a visits/flower ratio of 0.36:1. Just 38 morphospecies were encountered here, with Coleoptera contributing 52.3% of these visits (Table 1). Diptera comprised another 26.4% of the visits for this site type.

The total number of flowers observed in RGP.present sites was 2679, which is an average flower abundance of 546.2 flowers per site. *H. cymosum* flowers was most abundant, with 45.9%, while *S. bupleuroides* were 25.3% and *H. pallidum* 23.2% of the total flowers for this site type. Only 5 flower species were observed in RGP.present sites (Table. 2). RGP.present sites received an average of just 27.2 visits per site, and a visits/flower ratio of only 0.25:1. Thirty four morphospecies were observed, of which Coleoptera and Diptera represented 36% each. Lepidoptera was absent from RGP.present sites (Table 1).

When examining the FVNs of the different site types, it is clear that butterflies are affected by invasion of *R. cuneifolius* within PAs and RGPs (Fig. 2). Within PAs, most of the flower-visitors that interact with *Helichrysum cymosum*, the dominant focal flowers species, are Lepidoptera (butterflies) (Fig. 2a), however, when invaded by *R. cuneifolius*, Diptera (flies) take over this interaction (Fig. 2c). Butterflies also seem to largely disappear from RGP's, even when no bramble is present (Fig. 2a and Fig. 2b).

Figure 1. Overall flower visitation network showing the interaction between the focal plant species and their flower-visitors for all sites. The width of the links is proportional to the number of interactions observed. A: Coleoptera; B: bees/Apoidea; C: wasps/Hymenoptera excl. bees; D: Diptera; E: Hemiptera; F: Lepidoptera; G: Culicidae. 1) *Helichrysum pallidum*, 2) *Helichrysum cymosum*; 3) *Senecio bupleuroides*; 4) *Senecio tamoides*; 5) *Acalypha peduncularis*; 6) *Pentanisia prunelloides*; 7) *Eriosema squarrosum*; 8) *Senecio elegans*; 9) *Lobelia flaccida*; 10) *Hypoxis hemerocallidea*.



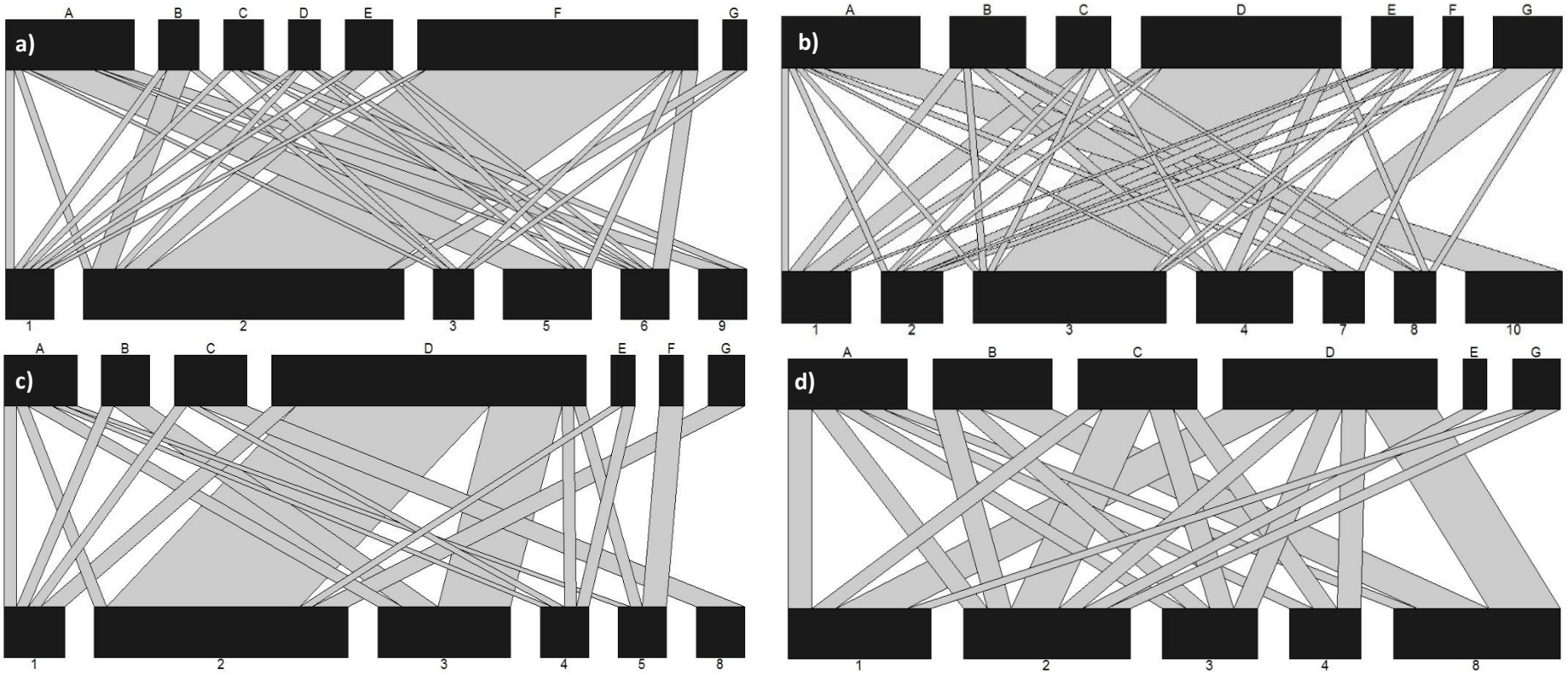


Figure 2. Flower-visitor interaction network structure for all sites of each site type; a) PA.absent, b) RGP.absent, c) PA.present, d) RGP.present. The width of the links is proportional to the number of interactions observed. A: Coleoptera; B: Apoidea; C: Hymenoptera excl. bees; D: Diptera excl. mosquitoes, E: Hemiptera; F: Lepidoptera; G: Culicidae. 1) *Helichrysum pallidum*, 2) *Helichrysum cymosum*; 3) *Senecio bupleuroides*; 4) *Senecio tamoides*; 5) *Acalypha peduncularis*; 6) *Pentanisia prunelloides*; 7) *Eriosema squarrosum*; 8) *Senecio elegans*; 9) *Lobelia flaccida*; 10) *Hypoxis hemerocallidea*.

Table 1. Percentage of morphospecies groups for each of the four site types; PA.absent- protected areas without *Rubus cuneifolius*; RGP.absent- within remnant grassland patches (RGP) without *R. cuneifolius*; PA.present- in protected areas with *R. cuneifolius*; RGP.present; in RGPs with *R. cuneifolius*. Also displayed is the overall percentage of flower-visitors that each site type contributed to the overall FVN, and the percentage of flower-visitors that each morphospecies group contributed to the overall FVN.

	PA.Absent	**RGP.Absent**	**PA.Present**	**RGP.Present**	**Overall**
Coleoptera	61.41	23.7%	61.4%	36.0%	41.6%
Diptera	8.68%	43.3%	8.68%	36.03%	29.03%
Hymenoptera	5.47%	7.82%	5.47%	9.56%	7.96%
Apoidea	2.89%	10.5%	2.89%	12.5%	7.09%
Hemiptera	4.50%	7.33%	4.50%	3.68%	5.53%
Lepidoptera	16.1%	4.16%	16.1%	0%	6.70%
Culicidae	0.96%	3.18%	0.96%	2.21%	2.14%
Overall	30.2	39.7	16.9	13.2	

Table 2. Percentage representation of focal flowers counted for each of the four site types; PA.absent- protected areas without *Rubus cuneifolius*; RGP.absent- within remnant grassland patches (RGP) without *R. cuneifolius*; PA.present- in protected areas with *R. cuneifolius*; RGP.present; in RGPs with *R. cuneifolius*. Also displayed is the overall percentage of flowers that each sites type contributes to the FVN, and the percentage of flowers that each focal flower species contributed to the overall FVN.

	PA.absent	**RGP.absent**	**PA.present**	**RGP.present**	**Overall**
Helichrysum pallidum	45.0%	46.2%	47.1%	23.2%	42.1%
Helichrysum cymosum	23.6%	21.3%	18.1%	45.9%	25.6%
Senecio bupleuroides	9.17%	11.5%	4.24%	25.3%	12.2%
Senecio tamoides	0.00%	15.8%	18.1%	3.62%	10.2%
Acalypha peduncularis	7.30%	0.00%	11.3%	0.00%	3.55%
Pentanisia prunelloides	14.4%	0.00%	0.00%	0.00%	3.54%
Eriosema squarrosum	0.00%	3.63%	0.00%	0.00%	1.55%
Senecio elegans	0.00%	1.39%	1.19%	1.94%	1.11%
Lobelia flaccida	0.57%	0.00%	0.00%	0.00%	0.14%
Hypoxis hemerocallidea	0.05%	0.18%	0.00%	0.00%	0.09%
Overall	24.6	42.7	15.6	17.14	

Effects of landscape impacts, forestry and *Rubus cuneifolius* infestation, on network-level indices

The focal flower species for the overall network share a mean number of 4.61 partners (Table 3). The overall network has a connectance of 0.22, a nestedness of 11.4, Shannon Diversity of 4.76 and a modularity of 0.20.

There was no significant difference in the mean number of shared partners for focal flower species for bramble, location, or the interactive effect of bramble and location (Table 3, Fig. 3a). There was no difference in connectance between sites where bramble was present and where it was absent, or between sites within PAs and RGPs (Table 3). The interactive effect of bramble and location on connectance was also not significant (Table 3, Fig. 3b). There was no significant difference in nestedness between sites within RGPs and sites within PAs, or between sites invaded by *R. cuneifolius* and those not invaded (Table 3). There was also no significant interactive effect between bramble and location on nestedness (Table 3, Fig. 3c).

There was a significant difference in modularity between bramble invaded and uninvaded sites (Table 3), with invaded sites exhibiting much lower modularity than uninvaded areas (Fig. 3d). There was no significant difference in modularity of sites based on location (whether in PA or RGP) and there were also no interactive effect between location and bramble (Table 3).

There was no significant difference in the Shannon Diversity of interactions between sites within RGPs and sites in PAs (Table 3, Fig. 3e), or between sites invaded by bramble and those not invaded. There were also no interactive effects between bramble and location on Shannon Diversity of interactions (Table 3).

Table 3. F value and significance of the landscape impacts, bramble (present or absent) and location (RGP or PA) as well as their interaction, on each flower-visitor measure, obtained by performing linear models.

	Source of Variation	**F**	***p***
Shared partners (flowers)	Bramble	0.13	0.719
	Location	2.17	0.159
	Bramble*Location	0.98	0.428
		F	***p***
Connectance	Bramble	0.72	0.406
	Location	1.40	0.252
	Bramble*Location	0.68	0.577
		F	***p***
Weighted NODF	Bramble	1.25	0.279
	Location	1.55	0.230
	Bramble*Location	0.94	0.449
		F	***p***
Modularity	Bramble	5.29	0.034*
	Location	0.03	0.858
	Bramble*Location	1.69	0.210
		F	***p***
Shannon Diversity	Bramble	0.00	0.985
	Location	0.60	0.448
	Bramble*Location	0.43	0.733

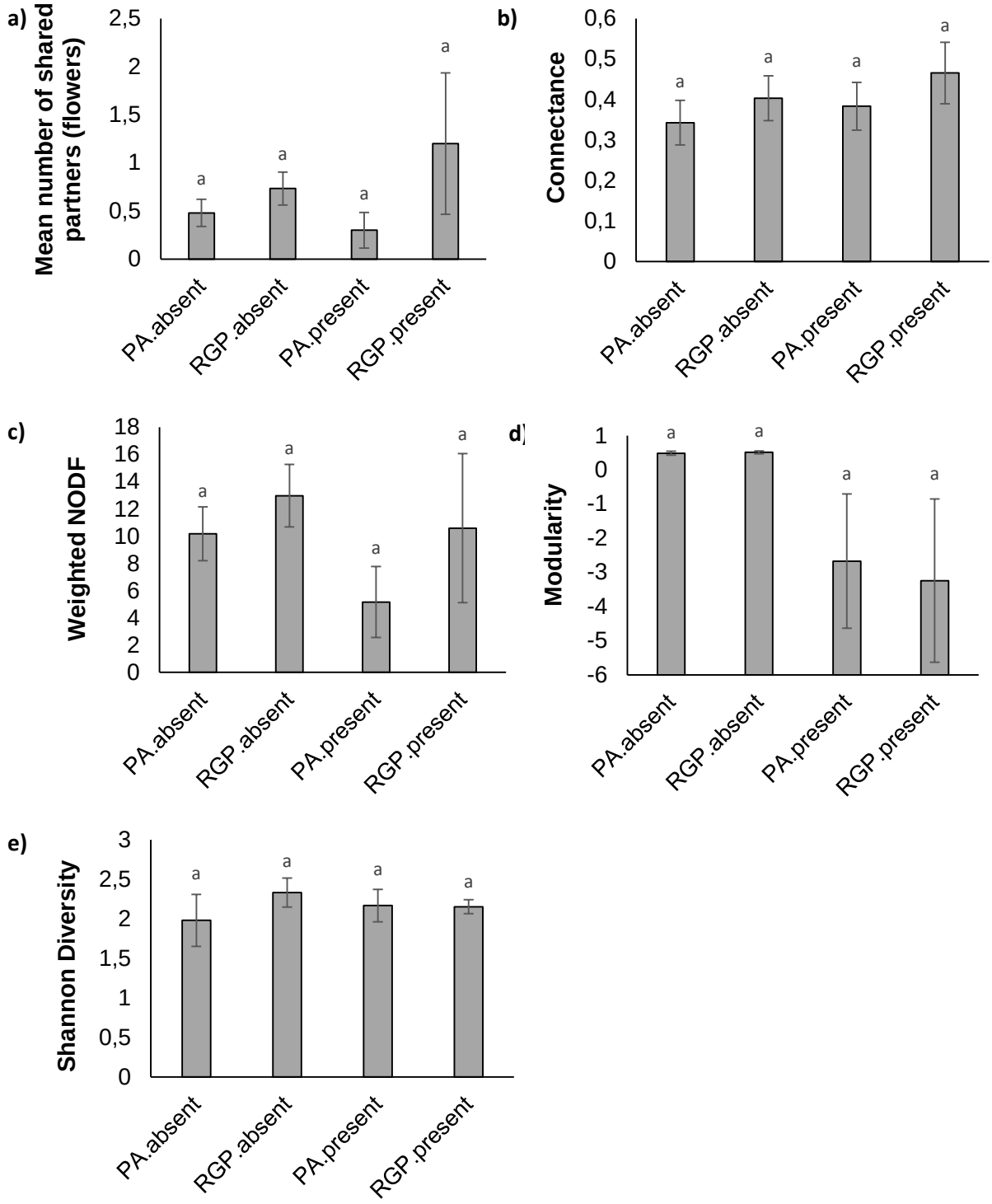


Figure 3. Network-level indices based on the landscape impacts location (PA or RGP) and *Rubus cuneifolius* (absent or present), for the four site types: RGP.absent- remnant grassland patches without bramble, PA.present- PA, invaded by bramble, RGP.present- RGP invaded by bramble.

Discussion

In the face of the current biodiversity crisis, any knowledge that will allow us to minimise loss of biodiversity is crucial. Knowledge on interaction networks does just that, and allows us to better understand the ways in which ecosystems are affected by loss of species. The structure of these networks can provide information regarding the robustness and resilience of ecosystems (Dunne et al., 2002a; Thébault & Fontaine, 2010). With better understanding of these networks comes the ability to better manage ecosystems to conserve biodiversity. Interaction webs provide complex depictions of biodiversity, species interactions, as well as ecosystem structure and function (Dunne et al., 2002a). Here I show that the complexity and organization, and therefore stability, resilience and robustness, of grassland ecosystems were not negatively influenced by nearby plantation blocks, but rather by the presence of invasive bramble.

The mean number of shared partners for both flower-visitors and focal flower species, connectance, nestedness and Shannon diversity were not affected by either location (whether the site was located in a PA or an RGP) or bramble (whether it was present or absent), or the interactive effects of the two factors. Modularity was affected by bramble but not location. Thus, it is clear that forestry plantations do not negatively affect the number of flower-visitors to the focal native plant species within the RGPs included in this study. However, bramble seems to be detrimental in these systems, especially within RGPs.

When examining the overall FVN of this system, it is clear that Diptera and *Senecio bupleuroides* have a very strong interaction. This indicates some specialisation in the system. Butterflies are sensitive to invasion by bramble within both PAs and RGPs. When PAs are invaded by bramble, butterflies are largely replaced with flies. Butterflies are also largely absent in RGPs within commercial forestry plantations, as opposed to sites within the PA. This is consistent with studies showing that butterflies are good indicators of the condition of biodiversity within transformed ecosystems (Brown & Freitas, 2000; Biological Record Center, 2006). Therefore, habitat quality is reduced by bramble invasion and by commercial forestry plantations.

The mean number of shared partners for focal flower species is the number of flower-visitors that each focal flower species shared. Because flowering often occurs simultaneously in plant communities, it is likely that co-flowering species will compete for pollinators (Rathcke, 1984).

Competition is best avoided by flowers through specialization, which leads to a reduction in the sharing of pollinators (Waser, 1983; Rathcke, 1984). The mean number of shared partners for focal flower species was not affected significantly by bramble invasion or location within RGPs. This is indicative that specialisation of flowers is not significantly different across the site types in this study. However, this could be attributed to the fact that only 10 focal flower species were considered here, and the species chosen were the most common species in the study areas, meaning that highly specialised plant species were likely excluded.

Connectance, described as the proportion of all possible interactions within a system that are realised, is thought to improve the stability of communities (Gardner & Ashby, 1970; Dunne et al., 2002b). This is because as the number of links in an interaction network increase, the impact of population fluctuations in that species will be minimised (Dunne et al., 2002b). This suggests that more complex communities with many highly connected species will be more stable to outside influence than simple communities with fewer highly connected species (Dunne et al., 2002b). Thus, within webs, increasing connectance should also increase the stability of the ecosystem (O'Gorman et al., 2010). High connectance, in general, is also indicative of pristine networks (Dunne et al., 2002a; Thébault & Fontaine, 2010). The connectance of this grassland ecosystem was not affected by invasion of *R. cuneifolius* nor by being located within RGPs, and neither by the interactive effects of invasion and forestry. The overall network as well as those for all of the site types was highly connected when compared to Martinez (1992) who calculated the mean connectance for five reliable sets of community interaction networks. Therefore, it is shown that these networks maintain their structure, even when invaded by bramble and when fragmented by forestry.

Nestedness represents a general measure of unevenness in the breadth of interactions; with highly nested networks generally comprised of both generalists and specialists, where specialist species interact mostly with generalist species and not with other specialists (Bahram et al., 2014). It has been found that most interaction networks, both trophic and mutualistic, are nested to some degree, and that the nested structure of mutualistic networks may contribute to the persistence of these networks from outside influences (Bascompte et al., 2006; Ulrich et al., 2009; Bahram et al., 2014). Nestedness was not affected by the location of sites (be they in PAs or RGPs), or by the invasion of bramble. It was also not affected by the interactive effect of alien and bramble. The overall FVN for this grassland ecosystem is rather highly nested, indicating that this ecosystem is well organized. An organized system refers to a system where

less abundant and specialised interactions are subsets of more abundant and generalised interactions (Castro-Urgal et al., 2012). Organization within ecosystems represents stability, and this in turn indicates that these ecosystems are more resilient to change and disturbance.

The invasion of bramble had a significantly negative effect on the modularity of the flower visitation networks for the grassland ecosystem. Modularity indicates network compartmentalization, whether interactions are more common within compartments than between compartments (Bahram et al., 2014). If an interaction network is modular, it indicates that within the network there are different groups of nodes performing different functions, and these groups have some degree of independence from one another (Holme et al., 2002; Guimerà & Amaral, 2005). It is, therefore, accepted that the modularity of complex mutualistic networks plays a critical role in their functionality, and that modularity increases robustness, flexibility, and stability of ecosystems (Hartwell et al., 1999; Guimerà et al., 2004). Therefore, the invasion by *R. cuneifolius* is detrimental to these grasslands because it reduces modularity, and by extension, the ability of the ecosystem to cope with disturbances, reducing the conservation value of the landscape and putting the biodiversity at risk. As found in chapter 2, flower-visitor assemblages were affected by the invasion of bramble, with a reduction in specialist flower-visitor species. Butterflies, a well-known indicator of ecological condition, were reduced within both PAs and RGPs when invaded by bramble, and absent when RGPs were invaded. Many previous studies assessing butterfly diversity and abundance have found that butterflies decline when there is invasion by alien plant species (Skórka et al., 2007; Florens et al., 2010). This is consistent with the findings that the modularity, and therefore the conservation value of the ecosystem, is decreased by the invasion of bramble, particularly within RGPs, due to the negative effects it has on flower-visitors.

Species diversity is one of the basic concepts of ecology that has been used in the characterisation of communities and ecosystems (De Jong, 1975). It is a long-held belief that diversity enhances community resistance to biological invasions (Levine & D'Antonio, 1999; Elton, 2000), supported by both theoretical (Robinson & Valentine, 1979; Case, 1990) and practical experiments (Stachowitz, 1999; Symstad, 2000). It was found by Garibaldi et al. (2013) that the management of an area to promote a high diversity of flower-visitors has great potential to improve the global yield of crops. This can be applied here to the functioning and conservation value of the remnant grassland areas within commercial forestry plantations. The Shannon Diversity Index combines the number of species within a site with the relative abundance of each species (Blair & Launer, 1997). Shannon diversity was not negatively

affected by the invasion of bramble, or by being located within RGPs instead of PAs, or by the interactive effect of the two factors. In a landscape mosaic of grasslands, natural forests and pine plantations, Pryke et al. (2013) found higher dung beetle diversity within the grasslands and the plantations. However, several other studies in the same system as this study also found that remnant patches had similar arthropod diversity levels as PAs (Samways et al., 2010; Pryke & Samways, 2012a; Pryke & Samways, 2012b). Therefore, it can be concluded that these RGP remain diverse despite their disturbances, although diversity alone does not take into consideration a change in species assemblage

Flower visitation networks seem to be largely unaffected by plantation blocks in RGPs, but were affected by alien bramble. Connectance, nestedness, and Shannon diversity were unaffected, which suggests that RGPs are effective and that the networks are able to maintain their structure despite the presence of *R. cuneifolius*. However, modularity was reduced substantially by the presence of bramble, and flower-visitor interactions were particularly low when bramble was within RGPs. This indicates that the invasive species does negatively affect overall FVNs, particularly within a fragmented system. Butterflies were reduced within invaded areas, and absent within invaded RGPs, suggesting that the quality of these habitats are reduced. This is indicative that the organization and complexity, and therefore robustness, of these ecosystems are somewhat affected by RGPs, but largely by the invasion of *Rubus cuneifolius*. This leaves them at a higher risk of extinctions during disturbance events than uninvaded areas. If bramble is left to spread and grow, the complexity of these FVNs may further decrease, reducing the resistance of these ecosystems to extinction. *R. cuneifolius* has been known to have negative effects on the diversity of grassland bird species, and is a serious threat to specialist grassland taxa (Reynolds & Symes, 2013). Therefore, it is of vital importance that bramble be cleared.

Here I show that flower visitation network indices in RGPs were not significantly different to those of PAs, suggesting that flower-visitor networks are largely maintained in these well connected patches. The largest impact remains the invasion of an alien flowering species which disrupts the pollination networks, reducing the conservation value of both PAs and RGPs. The eradication of the invasive alien species, *R. cuneifolius*, must be prioritised in order to ensure complex, robust and stable ecosystems which are resistant to outside disturbance in the face of a biodiversity crisis.

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CHAPTER 4
Conclusion

The effect of *Rubus cuneifolius* and commercial timber production on native grassland flower visitation

In this thesis, I set out to determine how the conservation value of grassland ecosystems is affected by commercial timber plantations and the invasive alien plant *Rubus cuneifolius* (American bramble). I expected conservation value of grasslands to be decreased by forestry plantations, and also decreased by the invasion of *R. cuneifolius*. In Chapter 2, I tested this by evaluating compositional changes in grassland ecosystems by measuring flower-visitation, flower-visitor diversity, as well as flower diversity and abundance of naturally occurring grassland plants within various landscape contexts; 1) uninvaded protected areas (PAs), 2) uninvaded remnant grassland patches (RGPs), 3) PAs invaded by *R. cuneifolius*, and 4) RGPs invaded by *R. cuneifolius*. This study found that flower abundance was increased within RGPs, but flower diversity, flower-visitor abundance and flower-visitor diversity were not significantly affected. Flower assemblages were not affected by any factors. However, flower-visitor assemblages were significantly affected by location (whether sites were within RGPs or PAs), and also by the invasion of bramble and the interaction between bramble and location. Specialisation of flower-visitors was affected by invasion by bramble, with an increase in generalist pollinators and a decrease in specialists in invaded areas, particularly RGPs.

In Chapter 3, I investigated how the complexity, stability and robustness of flower visitation networks of grassland ecosystems are affected by commercial timber plantations and the invasive alien plant *Rubus cuneifolius*. I anticipated these network properties to be negatively affected by both commercial timber plantations and the invasive alien plant *R. cuneifolius*. I tested this by evaluating interaction networks of naturally occurring grassland plants by constructing flower visitation networks of grassland areas within four landscape contexts; uninvaded PAs, uninvaded RGPs, invaded PAs and invaded RGPs. When examining the overall FVN of this system, it is clear that Diptera and *Senecio bupleuroides* have a very strong interaction, indicating some specialisation in the system. Butterflies were largely replaced by flies within PAs and RGPs when there was bramble invasion, and completely absent in invaded RGPs. This is indicative that the quality of these habitats is reduced compared to uninvaded PAs. Most network indices were unaffected by the presence of bramble and the location of the site, however, modularity was greatly reduced by the presence of bramble. This indicates a

reduction in complexity and organization. Ecological complexity, indicated by modularity, of flower visitation networks was significantly different for invaded and uninvaded areas, but was not affected by location (whether the sites were in PAs or RGPs). The invasion of bramble affects ecological complexity by affecting the flower-visitors within the flower visitation networks. These results show that RGPs contribute to biodiversity conservation by promoting ecological complexity despite exhibiting reduced habitat quality and complexity. However, invasive *R. cuneifolius* reduces ecological complexity of both RGPs and PAs and leads to reduced habitat quality in the areas that it invades.

After investigating the effects of fragmentation by commercial forestry plantations, and the invasion by *R. cuneifolius*, I found that RGPs are successful conservation tools, although species composition and specialisation are affected within them, and that bramble affects the flower-visitor assemblage composition (Chapter 2) as well as the network structure of flower-visitor interactions (Chapter 3). The connected nature of the RGPs within commercial forestry plantations work to ameliorate the negative effects of land transformation and fragmentation on the flower visitation of the grasslands of the KwaZulu-Natal Midlands, and flower visitation networks are largely maintained in these habitat fragments. However, the invasion of the alien invasive species, *R. cuneifolius*, affects species composition and disrupts pollination networks. There is also evidence that the effects of invasion by bramble are aggravated within RGPs.

Do connected RGPs minimise the effects of habitat fragmentation, and what is the effect of *R. cuneifolius*?

Within ecosystems, there are no organisms that exist in isolation (Tylianakis et al., 2010). The interactions between organisms form intricate networks, which provide information about which species link with which others, and the strength of these interactions (Montoya et al., 2006). These interaction networks are constructed to create better understanding about the functioning, the resilience and the robustness of the ecosystem (Dunne et al., 2002; Ings et al., 2009; Thébault & Fontaine, 2010). Therefore, it makes more ecological sense to study interaction networks than to use species approaches for conservation purposes. Pollination, one of our planets most vital services, is increasingly being analysed through the application of interaction network approaches to plant–pollinator communities (Kearns et al., 1998; Bascompte & Jordano, 2007; Baldock et al., 2011). A better understanding of the plant-pollinator systems of ecosystems, particularly those within transformed landscapes, will

provide information essential to their conservation (Carvalheiro et al., 2008). For these reasons, flower visitation networks were the analysis method chosen for this study.

In Chapter 2, I found that flower abundance differed between sites. Flower abundance was affected by location and also by the interactive effects of bramble and location. It was greatest in RGP.absent sites and lowest in PA.absent sites, indicating that the fragmentation caused by commercial forestry plantations doesn't negatively affect flower abundance. It is, however, likely that factors such as soil nutrients or water availability, not presence of plantations, are responsible for the increased flower abundance due to spatial autocorrelation that was found for flower abundance. Bramble was found to negatively affect flower abundance within RGPs, as in the presence of bramble, RGPs no longer have greater flower abundance than PAs. Flower diversity, flower-visitor abundance and flower-visitor diversity were unaffected by location or bramble. The flower-visitor species composition was altered significantly by commercial forestry plantations because land transformation has been found to be particularly disruptive to insect assemblages, particularly specialist species. Flower-visitor assemblages were also significantly affected by the invasion of bramble due to the effects that plant structure and floral-traits have on flower-visitors. Flowering plant species composition remained unaffected for all sites. Therefore, the composition of flower-visitor assemblages are more sensitive to habitat change than the flower assemblages. RGPs maintain most biodiversity, although with an altered, more generalist, flower-visitor assemblage, and bramble is detrimental to these ecosystems, especially within RGPs. With the loss of pollinating species, there is also a risk of extinction for plant species (Bond, 1995). So, although RGPs maintain most of the biodiversity, the reduction in specialist flower-visitors emphasises the importance of PAs for the conservation of all species.

In Chapter 3, I found that the mean number of shared partners for focal flower species, connectance, nestedness and Shannon diversity were not affected by either location (whether the site was located in a PA or an RGP) or bramble (whether it was present or absent), nor by their interactive effects. This shows that these networks largely maintain their structure despite invasion by bramble and fragmentation by forestry. Modularity was negatively affected by bramble, but location had no effect. Therefore, fragmentation caused by forestry plantations does not negatively affect number of flower-visitors which focal flowers species receive. The type of visitor received, however, is affected as butterflies are largely replaced with flies in invaded areas, and completely absent in invaded RGPs. Invasion by *R. cuneifolius* is

detrimental to grassland ecosystems, reducing modularity, and therefore the resilience of the ecosystem. This reduced ability to cope with disturbance means that the conservation value of these ecosystems is decreased, and puts the biodiversity at higher risk of extinction.

In this study, I have shown that remnant grassland patches within commercial forestry plantations do decrease the negative effects of land transformation on the flower visitation of the grasslands of the KwaZulu-Natal Midlands. Although the flower-visitor species composition is affected, RGPs maintain more biodiversity than would be present were these areas fully transformed and are, therefore, valuable for conservation. However, the results of this study highlight how critical it is to keep the RGPs clear of alien invasive plants, particularly *R. cuneifolius*. The effects of bramble invasion are particularly prominent within RGPs, as opposed to PAs, and invaded RGPs have lower conservation value than uninvaded RGPs.

Management recommendations

The fact that the forestry industry has set aside so much land for conservation is a victory in itself. Research up to this point has indicated that these areas have been successful for conservation of biodiversity and ecosystem function (Samways et al., 2010; Pryke & Samways, 2012a; Pryke & Samways, 2012b; Pryke et al., 2013). Due to the positive influence that RGPs have on conservation in fragmented and transformed landscapes, it is critical that these unplanted areas are retained. Furthermore, due to the sensitivity of these areas to disturbance, the quality of these habitats should be maximised to improve their effectiveness, and it should, therefore, be a priority to keep these areas pristine.

R. cuneifolius is a category 1 alien invasive plant within South Africa according to The Conservation of Agricultural Resources Act (CARA, 1983), which means that all plants must be removed & destroyed immediately. Category 1 invasives may not occur on any land or inland water surface other than in biological control reserves, must be controlled by the land user on whose land or inland water such plants are growing, may not be planted or propagated, may not be imported or sold, and may not be acquired (CARA, 1983). Therefore, not only because of the drastically negative effects of *R. cuneifolius* on grassland ecosystems, particularly within RGPs, but to comply with legislation, the removal of bramble must be a management priority.

Study limitations

There is a geographic bias in the location of study sites. All PA sites are clustered further south than RGP sites. The RGP sites are more dispersed throughout the entire commercial forestry plantation. Therefore, it is possible that any difference detected between PA and RGP sites is due to geographic position rather than whether the site was invaded or uninvaded, or managed as a PA or RGP.

The brambles themselves were unfortunately not sampled for this study, which could possibly have provided more information on their effects within flower visitation networks.

The method chosen for the measurement of flower abundance in this study, where a floral unit included both flowers and pseudanthia (a grouping of a few to thousands of flowers in a flower-like structure), could have biased the results of this study. This is because a flower can support one flower-visitor, while a pseudanthium can support many. A better suited method would have been to measure flower abundance in cm^2 in order for the number of visitors that a floral unit can support to be constant across plant species (Carvalheiro et al., 2014).

During the sampling period for this study, regrettably, only five sites each were sampled for invaded site types, while ten sites were sampled for each uninvaded site type. This was due to the bramble flowering season coming to an unexpected end. The uneven number of sites proved somewhat problematic during data analyses, and most statistical analyses were done excluding the extra five sites for uninvaded site types, using just five sites for all site types. This is lower than ideal for statistical analyses and may have resulted in some results not being significant, even when an emerging trend was observed, i.e. a type II error.

Although not a shortcoming, it should be mentioned that ten of the most popular focal flower species were used in the sample design for all the analyses. Due to this, the effects of rare plant species were essentially masked. Although the focus of this study was more on flower-visitors, this is something to consider when looking at the accuracy of the effect of bramble invasion and fragmentation caused by forestry plantation on native plant-species.

Further research

Flower visitation does not necessarily result in successful pollination and seed set (Vrdoljak, 2010), therefore following this study up with a study on the resulting seed set would generate understanding of what these effects mean for the ecosystem.

Invasion of *R. cuneifolius* within this transformed landscape has proven to be detrimental to these ecosystems and their FVNs, particularly within RGPs. Because of this, it has been determined that the removal of this invasive alien species is essential. A follow up study after the clearing would allow for a comparison, and in conjunction with this study, would provide useful knowledge for alien invasive clearing, particularly bramble, within forestry areas and other transformed landscapes.

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Appendix 1

List of all the sites within Gilboa Estate and Mount Gilboa Nature Reserve in KwaZulu-Natal, South Africa, as well as their global positioning system co-ordinates, location and status of invasion by *R. cuneifolius*. PA - Protected area; RGP - Remnant grassland patch; Ab – *R. cuneifolius* absent; Pr – *R. cuneifolius* present.

Site Name	Location	Invaded	Site Type	Latitude	Longitude
NV-PA1	PA	No	PA.Ab	-29.27633333	30.27776667
NV-PA2	PA	No	PA.Ab	-29.27878333	30.28623333
NV-PA3	PA	No	PA.Ab	-29.27763333	30.2838
NV-PA4	PA	No	PA.Ab	-29.27583333	30.27938333
NV-PA5	PA	No	PA.Ab	-29.27545	30.27688333
NV-PA6	PA	No	PA.Ab	-29.27418333	30.27516667
NV-PA7	PA	No	PA.Ab	-29.27901667	30.28905
NV-PA8	PA	No	PA.Ab	-29.27371667	30.2782
NV-PA9	PA	No	PA.Ab	-29.27278333	30.27643333
NV-PA10	PA	No	PA.Ab	-29.278	30.28106667
NV-RGP1	RGP	No	RGP.Ab	-29.2491	30.25173333
NV-RGP2	RGP	No	RGP.Ab	-29.25153333	30.32375
NV-RGP3	RGP	No	RGP.Ab	-29.24628333	30.27708333
NV-RGP4	RGP	No	RGP.Ab	-29.24711667	30.27451667
NV-RGP5	RGP	No	RGP.Ab	-29.24596667	30.2538
NV-RGP6	RGP	No	RGP.Ab	-29.2458	30.29703333
NV-RGP7	RGP	No	RGP.Ab	-29.24493333	30.30033333
NV-RGP8	RGP	No	RGP.Ab	-29.2515	30.31878333
NV-RGP9	RGP	No	RGP.Ab	-29.24558333	30.24526667
NV-RGP10	RGP	No	RGP.Ab	-29.24841667	30.24596667
AB-PA1	PA	Yes	PA.Pr	-29.2755	30.2793
AB-PA2	PA	Yes	PA.Pr	-29.27438333	30.27443333
AB-PA3	PA	Yes	PA.Pr	-29.2739	30.27816667
AB-PA4	PA	Yes	PA.Pr	-29.27851667	30.28806667
AB-PA5	PA	Yes	PA.Pr	-29.27738333	30.2813

AB-RGP1	RGP	Yes	RGP.Pr	-29.27633333	30.27776667
AB-RGP2	RGP	Yes	RGP.Pr	-29.27878333	30.28623333
AB-RGP3	RGP	Yes	RGP.Pr	-29.27763333	30.2838
AB-RGP4	RGP	Yes	RGP.Pr	-29.27583333	30.27938333
AB-RGP5	RGP	Yes	RGP.Pr	-29.27545	30.27688333

Appendix 2

List of focal flower species compiled by species- and family names, and numbers used for ease of analysis.

Number	**Species**	**Family**	**Flower Abundance**
1	*Helichrysum pallidum*	Asteraceae	6582
2	*Helichrysum cymosum*	Asteraceae	4050
3	*Senecio bupleuroides*	Asteraceae	2170
4	*Senecio tamoides*	Asteraceae	1324
5	*Acalypha peduncularis*	Euphorbiaceae	555
6	*Pentanisia prunelloides*	Rubiaceae	553
7	*Eriosema squarrosum*	Fabaceae	242
8	*Senecio elegans*	Asteraceae	174
9	*Lobelia flaccida*	Lobeliaceae	22
10	*Hypoxis hemerocallidea*	Hypoxidaceae	14

Appendix 3

List of flower-visitors recorded during November 2013-February 2014 at all sites. Flower-visitors were classified to order and a few have been further identified to separate them from others in the same order. Site/s column identifies within which site types the flower-visitor was observed: PA.Ab – protected area, *R. cuneifolius* absent; RGP.Ab – remnant grassland patch, *R. cuneifolius* absent; PA.Pr – protected area, *R. cuneifolius* present and RGP.Pr - remnant grassland patch, *R. cuneifolius* present.

Morphospecies	Order	Further ID	Number observed	%	Site/s
APO001	Hymenoptera	Bee	4	0.39	RGP.Ab, PA.Pr
APO002	Hymenoptera	Bee	6	0.59	PA.Ab, RGP.Ab, RGP.Pr
APO003	Hymenoptera	Bee	36	3.52	RGP.Ab, PA.Pr
APO004	Hymenoptera	Bee	3	0.29	PA.Ab, RGP.Ab
APO005	Hymenoptera	Bee	1	0.10	RGP.Ab
APO006	Hymenoptera	Bee	15	1.47	PA.Ab, RGP.Ab, RGP.Pr
COL001	Coleoptera	-	8	0.78	RGP.Ab
COL002	Coleoptera	-	26	2.54	PA.Ab, RGP.Ab, PA.Pr
COL003	Coleoptera	-	32	3.13	All
COL004	Coleoptera	-	2	0.20	PA.Ab, RGP.Ab
COL005	Coleoptera	-	44	4.31	All
COL006	Coleoptera	-	88	8.61	PA.Ab, RGP.Ab, PA.Pr
COL007	Coleoptera	-	5	0.49	PA.Ab, RGP.Ab
COL008	Coleoptera	-	1	0.10	RGP.Ab
COL009	Coleoptera	-	2	0.20	PA.Ab, RGP.Ab
COL010	Coleoptera	-	2	0.20	RGP.Pr
COL011	Coleoptera	-	24	2.35	PA.Ab, RGP.Ab, PA.Pr
COL012	Coleoptera	-	26	2.54	PA.Ab, RGP.Ab, PA.Pr
COL013	Coleoptera	-	1	0.10	RGP.Ab
COL014	Coleoptera	-	16	1.57	All
COL015	Coleoptera	-	1	0.10	RGP.Ab
COL016	Coleoptera	-	1	0.10	RGP.Ab

COL017	Coleoptera	-	1	0.10	RGP.Ab
COL018	Coleoptera	-	53	5.19	PA.Ab, RGP.Ab, RGP.Pr
COL020	Coleoptera	-	1	0.10	PA.Ab, RGP.Ab
COL022	Coleoptera	-	4	0.39	RGP.Pr
COL023	Coleoptera	-	2	0.20	RGP.Pr
COL024	Coleoptera	-	5	0.49	PA.Ab, RGP.Ab, RGP.Pr
COL025	Coleoptera	-	2	0.20	PA.Ab, RGP.Ab
COL026	Coleoptera	-	3	0.29	PA.Ab, RGP.Ab
COL028	Coleoptera	-	8	0.78	PA.Ab, RGP.Ab
COL029	Coleoptera	-	6	0.59	PA.Ab, RGP.Ab
COL030	Coleoptera	-	1	0.10	PA.Ab, RGP.Ab
COL031	Coleoptera	-	4	0.39	PA.Ab, RGP.Ab
COL032	Coleoptera	-	2	0.20	RGP.Ab, PA.Pr
COL033	Coleoptera	-	2	0.20	RGP.Ab, PA.Pr
COL034	Coleoptera	-	1	0.10	PA.Pr
COL035	Coleoptera	-	2	0.20	PA.Pr
COL036	Coleoptera	-	5	0.49	PA.Pr
COL039	Coleoptera	-	22	2.15	All
COL040	Coleoptera	-	2	0.20	PA.Ab, RGP.Ab
COL041	Coleoptera	-	1	0.10	PA.Ab, RGP.Ab
COL042	Coleoptera	-	3	0.29	PA.Pr, RGP.Pr
COL043	Coleoptera	-	1	0.10	RGP.Ab
COL044	Coleoptera	-	2	0.20	RGP.Ab
COL045	Coleoptera	-	3	0.29	RGP.Ab
COL046	Coleoptera	-	1	0.10	RGP.Ab
COL047	Coleoptera	-	3	0.29	PA.Ab, RGP.Ab
COL048	Coleoptera	-	2	0.20	PA.Ab, RGP.Ab
COL049	Coleoptera	-	1	0.10	PA.Ab, RGP.Ab
COL050	Coleoptera	-	2	0.20	PA.Ab, RGP.Ab
COL052	Coleoptera	-	3	0.29	RGP.Pr

COL054	Coleoptera	-	1	0.10	RGP.Ab
CUL001	Diptera	Mosquito	11	1.08	All
CUL002	Diptera	Mosquito	4	0.39	RGP.Ab
CUL004	Diptera	Mosquito	7	0.68	RGP.Ab
DIP002	Diptera	-	50	4.89	PA.Ab, RGP.Ab, RGP.Pr
DIP003	Diptera	-	17	1.66	PA.Pr
DIP004	Diptera	-	3	0.29	PA.Ab, RGP.Ab, RGP.Pr
DIP005	Diptera	-	87	8.51	PA.Ab, RGP.Ab, RGP.Pr
DIP006	Diptera	-	11	1.08	All
DIP007	Diptera	-	11	1.08	PA.Pr, RGP.Pr
DIP008	Diptera	-	1	0.10	RGP.Ab
DIP009	Diptera	-	37	3.62	PA.Ab, RGP.Ab. PA.Pr
DIP010	Diptera	-	1	0.10	RGP.Pr
DIP011	Diptera	-	4	0.39	PA.Pr
DIP012	Diptera	-	4	0.39	PA.Ab, RGP.Ab, RGP.Pr
DIP014	Diptera	-	14	1.37	PA.Ab, RGP.Ab, RGP.Pr
DIP015	Diptera	-	7	0.68	RGP.Pr
DIP016	Diptera	-	6	0.59	PA.Ab, RGP.Ab, RGP.Pr
DIP017	Diptera	-	7	0.68	PA.Ab, RGP.Ab. PA.Pr
DIP019	Diptera	-	3	0.29	PA.Ab, RGP.Ab. PA.Pr
DIP020	Diptera	-	5	0.49	PA.Ab, RGP.Ab. PA.Pr
DIP021	Diptera	-	7	0.68	PA.Ab, RGP.Ab
DIP023	Diptera	-	5	0.49	PA.Ab, RGP.Ab
DIP025	Diptera	-	1	0.10	PA.Ab, RGP.Ab
DIP026	Diptera	-	8	0.78	PA.Ab, RGP.Ab
DIP027	Diptera	-	6	0.59	All
DIP028	Diptera	-	2	0.20	PA.Ab, RGP.Ab. PA.Pr
DIP029	Diptera	-	1	0.10	PA.Pr

DIP030	Diptera	-	1	0.10	PA.Pr
HEM002	Hemiptera	-	2	0.20	PA.Pr
HEM003	Hemiptera	-	2	0.20	PA.Ab, RGP.Ab
HEM004	Hemiptera	-	28	2.74	All
HEM005	Hemiptera	-	1	0.10	RGP.Ab
HEM006	Hemiptera	-	6	0.59	All
HEM008	Hemiptera	-	6	0.59	PA.Ab, RGP.Ab, RGP.Pr
HEM009	Hemiptera	-	2	0.20	PA.Ab, RGP.Ab
HEM013	Hemiptera	-	6	0.59	PA.Ab, RGP.Ab
HEM014	Hemiptera	-	1	0.10	PA.Ab, RGP.Ab
HEM015	Hemiptera	-	1	0.10	PA.Ab, RGP.Ab
HEM016	Hemiptera	-	1	0.10	RGP.Ab
HEM017	Hemiptera	-	1	0.10	RGP.Ab
HYM002	Hymenoptera	Wasp	1	0.10	RGP.Ab
HYM003	Hymenoptera	Wasp	9	0.88	RGP.Ab, PA.Pr
HYM005	Hymenoptera	Wasp	10	0.98	PA.Ab, RGP.Ab
HYM006	Hymenoptera	Wasp	10	0.98	All
HYM007	Hymenoptera	Wasp	10	0.98	PA.Pr, RGP.Pr
HYM008	Hymenoptera	Wasp	32	3.13	All
HYM009	Hymenoptera	Wasp	1	0.10	PA.Ab, RGP.Ab
HYM010	Hymenoptera	Wasp	3	0.29	PA.Ab, RGP.Ab, PA.Pr
HYM014	Hymenoptera	Wasp	2	0.20	PA.Pr, RGP.Pr
HYM015	Hymenoptera	Wasp	2	0.20	RGP.Ab
HYM016	Hymenoptera	Wasp	2	0.20	RGP.Ab
LEP001	Lepidoptera	-	4	0.39	RGP.Ab
LEP002	Lepidoptera	-	5	0.49	RGP.Ab
LEP003	Lepidoptera	-	1	0.10	PA.Ab, RGP.Ab
LEP004	Lepidoptera	-	2	0.20	PA.Ab, RGP.Ab
LEP005	Lepidoptera	-	3	0.29	PA.Ab, RGP.Ab
LEP006	Lepidoptera	-	2	0.20	PA.Ab, RGP.Ab

LEP008	Lepidoptera	-	52	5.09	PA.Ab, RGP.Ab, PA.Pr